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PHYLOGENETIC HYPOTHESES OF THE RELATIONSHIPS OF ARTHROPODS TO PRECAMBRIAN AND CAMBRIAN PROBLEMATIC FOSSIL TAXA

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Abstract.—A number of Vendian (latest Precambrian) body fossils have traditionally been considered arthropods or arthropodlike organisms. Several Cambrian “weird wonders” have also been linked with the arthropods. However, these relationships are difficult to express in traditional Linnean systematics. I present a morphological cladistic analysis of seven Vendian “arthropodlike” taxa compared with 21 representative Cambrian arthropods, lobopods, and weird wonders. Four arthropods from the later Phanerozoic (a pycnogonid, a monuran, and the problematic *Cheloniellon* and *Arthropleura*), five extant tardigrades, two extant kinorhynchs, and an extant priapulid, myriapod, pycnogonid, and onychophoran are also included. Monophyly of the Arthropoda is supported, but the anomalocarids and their relatives (Anomalopoda) fall out very close to the base of the traditional Arthropoda and should be included within it. The relationships among arthropods with uniramous appendages are not well resolved, but the group does not appear to be monophyletic. The biramous arthropods do form a clade and are divided into a crustaceanomorph clade and an arachnomorph clade that includes the trilobites. Most Vendian arthropodlike fossils form two clades, the Vendiamorpha and the Sprigginidae, in the arthropod stem group. The Lobopoda is a monophyletic clade with three branches: tardigrades, onychophorans, and marine lobopods. An unranked taxonomic scheme is proposed for the major clades identified here. There is no compelling reason to accept the hypothesis that the Vendian organisms included here are not metazoans. [Precambrian; Vendian; Ediacara fauna; Cambrian; problematica; arthropod; lobopod.]

There is something about writing about arthropod phylogeny that brings out the worst in people.

—J. W. Hedgpeth (Schram, 1981)

The soft-bodied megafossils of the Vendian or Ediacaran (late Precambrian or Neoproterozoic) have classically been considered metazoans in extant phyla, often in or near extant classes or orders (e.g., Glaessner, 1984). However, a number of dissenting opinions place most or all of these fossils in an extinct kingdom Vendobionta (Seilacher, 1989, 1992; Bergström, 1991), an extinct metazoan phylum (Buss and Seilacher, 1994), or an extant nonmetazoan kingdom (e.g., Zhuravlev, 1993; Retallack, 1994), thereby denying them any direct significance for early metazoan evolution. Obstacles to considering the “Vendobionta” as early metazoans include the time gap between the disappearance of Vendian biotas and the appearances of Cambrian faunas, the lack of Vendian-type soft-bodied organisms in the Cambrian and later *Lagerstätten*; and supposed mor-

phological disparity between most Vendian organisms and their Phanerozoic successors.

Resolution of this debate would be desirable, because our understanding and interpretation of the Precambrian–Cambrian transition is colored by our taxonomic pronouncements. The magnitude of whatever extinction took place between the Vendian and Cambrian is an example of this. If the Vendian organisms form a monophyletic kingdom Vendobionta, with a *Bauplan* fundamentally different from anything known from the Phanerozoic, then obviously an extinction event separates the Vendian and Cambrian. In fact, if the Vendobiontan hypothesis (Seilacher, 1989, 1992) is correct, the largest mass extinction in history separates the Vendian and Cambrian, at least in terms of the rank of the taxa that it claimed; no other mass extinction, as far as we know, has destroyed an entire kingdom. Any number of scenarios can be devised for said extinction, from vulcanism or bolide impact (Felitsyn et al., 1989) to

the evolution of predators (McMenamin, 1986; Seilacher, 1989). However, if the Vendian organisms were early representatives of several extant taxa, then the presumed extinction event loses magnitude: perhaps the difference between Vendian and Cambrian biotas is due more to rapid diversification and pseudoextinction, possibly coupled with changes in taphonomic conditions, than to mass extinction in the usual sense. It is therefore important to document and test all possible cases of phylogenetic continuity across the Precambrian–Cambrian boundary. In the absence of a complete fossil record, this is the only way to assess the true significance of the Vendian fossils for the Phanerozoic history of metazoans.

A time gap in the fossil record of a presumed clade does not by itself disprove relationship; e.g., the 65 million year gap between the youngest fossil coelacanth and *Latimeria chalumnae*. At most Vendian localities, the interval between the Vendian and Cambrian assemblages is obscured by unconformities (reviewed by Jenkins, 1989; Conway Morris, 1993a) and/or facies change (e.g., Pirrus, 1992). Scarcity of Vendian-type preservation and faunas in later *Lagerstätten* is also not an obstacle. Although Burgess Shale-type *Lagerstätten* and their distinctive faunas disappear after the Cambrian (Allison and Briggs, 1991), this does not mean that the Burgess Shale organisms are unrelated to anything living and form the kingdom Burgess-Shale-*o'bionta*.

The third potential barrier to establishing links, morphological differences, is less easily surmounted. Documenting or disproving phylogenetic links between Vendian and Phanerozoic taxa is made difficult by rarity and poor preservation of key fossils and lack of characters for analysis. Thus, a number of Cambrian "medusoids" that have been claimed as Ediacaran survivors have turned out to be no such thing (Barskov and Zhuravlev, 1988; Dzik, 1991; Conway Morris, 1993a). Some past identifications, such as the identification of the Cambrian *Xenusion* as a Vendian-type "frondlike organism" (Tarlo, 1967; Mc-

Menamin, 1986; McMenamin and McMenamin, 1990), are probably ingeniously wrong (Dzik and Krumbiegel, 1989). Other Phanerozoic fossils seem to be comparable with Vendian forms, but a relationship cannot be confirmed because of poor preservation, morphological simplicity, or lack of study (e.g., Pickerill, 1982; Gehling, 1991).

Nevertheless, several lineages do seem to cross the boundary, including (1) two lineages of frondlike fossils, one of which is probably related to extant pennatulaceans (Conway Morris, 1993a), (2) probable sea anemones (Gehling, 1991; Conway Morris, 1993a), and (3) annulated discoidal fossils resembling hydrozoan chondrophorines (Conway Morris, 1993a; Waggoner and Collins, 1995). Vendian strata have also yielded a plausible echinoderm (Gehling, 1987), at least one sponge (Gehling, 1993), and a few jellyfishlike forms with definite fourfold symmetry (Fedonkin, 1985a, 1985b; Gehling, 1991). A number of trace fossil genera also cross the Vendian–Cambrian boundary (Fedonkin, 1985c), as do the sabelliditids, which may be pogonophoran relatives (Sokolov, 1968; Fedonkin, 1985a).

The problem of arthropod ancestors in the Vendian has not been settled. Nevertheless, Vendian fossils with a remarkable resemblance to trilobites have been found and illustrated, although not yet formally described (Gehling, 1991: pl. 4, fig. 4; Jenkins, 1992: fig. 15). Other Vendian arthropodlike fossils, such as *Praecambrium* and *Vendia*, have classically been considered arthropods or near-arthropods (Glaessner, 1984; Fedonkin, 1985a, 1985b; Gehling, 1991; Simonetta and Insom, 1993), whereas other workers have focused on differences between these forms and arthropods (e.g., Bergström, 1991; Hou et al., 1991). In this paper, I attempt to identify and support links between Cambrian and Vendian forms, using cladistic methods.

CONCEPTS AND METHODS

Weird Wonders: A Cladistic Definition

The term *weird wonder* was introduced by Gould (1989) and has since become a

common term for a fossil organism that lacks obvious similarities to any living taxon. In a cladistic sense, a weird wonder is an organism with numerous autapomorphies and few synapomorphies; an organism is not a weird wonder if it is only poorly preserved or poorly known (Yochelson, 1991). Both fossil and living organisms can be weird wonders (for some living ones, see Haszprunar et al., 1991). A living or fossil weird wonder for which synapomorphies are documented loses its weirdness: when *Hallucigenia* was reinterpreted as a marine lobopod (Ramsköld, 1992), it became possible to fit *Hallucigenia* into a systematic hierarchy. Weirdness may vary among levels in a hierarchical taxonomy. *Sagitta*, for instance, is not a weird chaetognath (it shares many synapomorphies with other chaetognaths) nor is it weird on the kingdom level (it has many animal synapomorphies). *Sagitta* is a weird wonder with respect to other invertebrate phyla because it shows few obvious synapomorphies with members of other phyla. Bengtson (1986:3) defined a phylum as "a group of organisms of uncertain taxonomic affinities, that is, a problematic taxon." In other words, a phylum is a weird wonder, i.e., an expression of ignorance as to the affinities of its constituent organisms with all others. The Vendian macrofossils are weird wonders indeed; they have been allied at various times with four out of the traditional five living kingdoms and with at least two extinct kingdom-level taxa.

This treatment of the Vendian fossils is an example of a general tendency in dealing with problematic fossil taxa, to treat them as belonging "nowhere among the known animals of this or any former earth" (Gould, 1989:134), with "no . . . persuasive clues to homology, or genealogical relationship with any other group of organisms" (Gould, 1989:193), whose "body-plans do not 'fit' any of the groups known either as fossils or as extant forms" (Hall, 1992:28), and so on. As Conway Morris (1993b:224) noted, Precambrian and Cambrian problematic fossils are "in imminent danger of elevation to a classic status as evolutionary enigmas." This approach is

having taxonomic repercussions; Burgess Shale fossils such as *Anomalocaris*, *Opabinia*, *Nectocaris*, and especially *Hallucigenia* (before it was inverted [Ramsköld, 1992]) are often cited as single species "worthy" of their own phyla. Anderson (1993) formally proposed eight monospecific phyla for Vendian and Cambrian weird wonders. Such a nihilistic taxonomy leaves no framework to address the questions of interrelationships among phyla; a phylum simply is. Erecting phyla for problematic organisms makes them no less problematic; shunting problematica into their own kingdoms or phyla is itself a form of "shoehorning" (Gehling, 1991). As has been shown for the Vendian organisms, such a taxonomy and such a view of weird wonders will color our perceptions of organismal diversification, extinction rate and magnitude, and even global ecology as much if not more so than shoehorning them into extant taxa. As Bengtson (1986: 4) wrote,

the concept [of the phylum], as based on living organisms, is not a suitable tool to analyze the history of metazoan diversification *except* under the assumption that present-day phyla represent the full or almost full spectrum of body plans available to animals and that phyla seldom or never become extinct.

Two things need to be done. First, problematic fossils must be incorporated into phylogenetic analyses. By definition, their synapomorphies with other taxa will not be obvious; these synapomorphies must be searched for and documented. Proposing homologies between weird wonders and well-known taxa may require some risk-taking, and the taxonomic position of weird wonders may be labile or uncertain; this is, however, preferable both to shoehorning them into extant taxa and to refusing to deal with their relationships.

Second, taxonomic schemes should be unranked (de Queiroz and Gauthier, 1992) or several ranks must be created between kingdom and phylum. Valentine (1973) took a step towards this by proposing that the rank of superphylum is useful for expressing relationships among animal phyla and could be used to accommodate the

Vendian organisms. The interrelationships between high-level clades can in principle be known; the problem is that in traditional Linnean taxonomy there is no standard way to express such relationships. When an organism cannot be shoehorned into any extant phylum, there is no alternative but to call it a weird wonder, with no relationship to any extant taxon. Although the organism must be related to extant organisms in some way, this relationship cannot be expressed in traditional Linnean taxonomy—and this may be quite misleading.

Vendian Fossils and Metazoan Phylogeny

Some scientists have objected to applying cladistics to problematic fossils. Simonetta (1990) claimed that in the early history of taxa there is a phase in which advanced characters are acquired repeatedly and at random by various members of the group, so that organisms appear as mosaics of advanced and archaic features and convergence is rampant; this situation will render the principle of parsimony useless. Gould (1989) proposed a similar "grab-bag" model for early metazoan evolution: the characters of weird wonders represent "a broad range of latent and recruitable structures" (1989:217) common to a wide range of metazoan lines. Such latent characters could be activated in genealogically distant lineages, again the result is rampant homoplasy.

These hypotheses are testable. If Simonetta's (1990) hypothesis or Gould's (1989) grab-bag model were true, consistency indices of cladograms that include weird wonders should be abnormally low: these predictions can be tested by doing the analysis. These hypotheses may justify the use of unordered characters, as Briggs et al. (1992; also Wills et al., 1994) used; it is probably better to avoid a priori judgments of character polarity when dealing with problematic organisms far back in time, especially if morphological evolution was less canalized because of a plethora of "latent recruitable structures" or relaxed genetic regulation (Valentine and Campbell, 1975).

A cladistic approach to problematic fossils avoids both the shoehorning of problematica into extant phyla and the phylogenetic agnosticism of erecting phyla for individual organisms. This approach may also give better resolution of the relationships among extant high-level metazoan clades; fossils are potentially important in phylogenetic reconstruction (reviewed by Donoghue et al., 1989; Smith, 1994). When rates of evolution are high or the time spans involved are long, the inclusion of even fragmentary fossils will improve cladogram resolution (Huelsenbeck, 1991). Metazoan phyla fulfil both of these criteria: they arose in a rapid burst of evolution and have been separated for at least 540 million years. If the radiation of a clade generates high homoplasy, then errors in phylogenetic analyses of extant members of the clade will result. Inclusion of fossil taxa that bracket the radiation may be the only way to minimize this source of error. There is therefore no reason not to use fossils, even problematic ones, in phylogenetic analyses.

A number of attempts have recently been made to apply cladistic methods to the systematics of weird wonders (Beall, 1991; Schram, 1991; Budd, 1993; Conway Morris and Peel, 1995; Hou and Bergström, 1995; Monje-Najera, 1995). A recent treatment of the Vendian biota (Buss and Seilacher, 1994) included cladistic terminology but lumped the Vendian biota into one terminal taxon and also relied on characters that are not preserved in fossils. The morphology of many of the Vendian organisms is so simple that getting enough characters is a problem, and many of the characters that such fossils do have are arguably plesiomorphies or convergences, if not taphonomic artifacts. In the case of the Vendian "medusoids," for instance, many of the characters needed for a meaningful comparison with living organisms are simply not seen in fossils. Cladistic analysis of the majority of Vendian organisms is therefore not feasible.

One set of Vendian organisms, however, shows sufficient morphological complexity for a meaningful comparison with Phan-

erozoic organisms, i.e., the proarticulates or protoarthropods, which are cephalized, seriated, bilaterally symmetrical organisms that have classically been considered arthropod relatives (Glaessner, 1984; Fedonkin, 1985a, 1985b). There is also a growing number of morphological analyses of Recent and fossil arthropods and related taxa (Bergström, 1992; Briggs and Fortey, 1992; Briggs et al., 1992; Eernisse et al., 1992; Wheeler et al., 1993; Wills et al., 1994; Hou and Bergström, 1995; Monje-Najera, 1995) and molecular analyses of extant arthropods (Lake, 1990; Erwin, 1991; Turbeville et al., 1991; Ballard et al., 1992; Winnepeninckx et al., 1992; Wheeler et al., 1993). Although there is hardly a consensus on arthropod phylogeny, this database at least provides a framework within which to compare analyses that include Vendian taxa.

PROCEDURE

Selection of Taxa

The Vendian taxa selected for cladistic analysis were *Praecambridium*, *Parvancorina*, *Vendia*, *Mialsemia*, *Bomakellia*, *Spriggina*, and *Marywadea*. *Praecambridium*, *Parvancorina*, and *Spriggina* are known from several specimens from the Ediacara Hills of south Australia and rare specimens from the White Sea coast of the northeastern Russian platform. *Marywadea* is currently known only from Ediacara, and *Vendia*, *Bomakellia*, and *Mialsemia* are known from single specimens from the White Sea coast. I scored most of these forms from literature descriptions (see Appendix 1) but had the opportunity to examine the holotypes of *Bomakellia*, *Mialsemia*, and *Vendia* and original material of *Parvancorina* and cf. *Praecambridium* and to score characters directly from them. I also examined casts of Ediacaran specimens of *Spriggina* and *Parvancorina* in the collections of the University of California Museum of Paleontology (Figs. 1a–c).

Cambrian taxa selected were the onychophoranlike *Onychodictyon*, *Hallucigenia*, *Xenusion*, *Microdictyon*, *Cardiodictyon*, *Lulishania*, and *Aysheaia*, the arthropods

Marrella, *Canadaspis*, *Olenoides*, *Agnostus*, *Naraoia*, *Sanctacaris*, *Burgessia*, *Yohoia*, *Leanchoilia*, *Skara*, and *Sidneyia*, and the problematic *Anomalocaris*, *Peytoia*, *Opabinia*, *Nectocaris*, *Facivermis*, and *Kerygmachela*. (Discoveries of complete anomalocarid fossils in China have made revision of the genus *Anomalocaris* necessary: former *Anomalocaris nathorsti*, the most common and best known Burgess Shale anomalocarid, has since been placed in the revived genus *Peytoia* [Chen et al., 1994], which should be kept in mind when referring to earlier literature on *Anomalocaris*. In this paper, the term "anomalocarid" refers to material for which the genus is not obvious or not specified.) I also included an unnamed Burgess Shale problematicum reconstructed by Delle Cave and Simonetta (1991: fig. 32C). I have drawn on their reconstruction for now (Fig. 1d), although no formal description has yet appeared. They dubbed the fossil "Collins's monster" after its discoverer; this form is referred to here as the C-monster, pending its formal description.

Four post-Cambrian fossil arthropods were included: the Devonian pycnogonid *Palaeoisopus*, the Carboniferous monuran *Dasyleptus*, and the two Devonian problematic arthropods *Arthropleura* and *Cheloniellon*. Eleven extant taxa were also scored: the priapulid *Priapululus*, the kinorhynch *Echinoderes* and *Semnoderes*, the heterotardigrades *Neostygarctus*, *Echiniscus*, and *Echiniscoides*, the eutardigrades *Milnesium* and *Macrobotus*, the onychophoran *Peripatus*, the pycnogonid *Nymphon*, and the centipede *Lithobius*. These taxa were included to increase the range of morphological diversity and to provide exemplars for taxa that are not known as fossils or not represented in the Cambrian. These taxa were scored from descriptions in the literature (Appendix 1).

There is already considerable evidence that the organisms chosen are likely to be related in some way. Delle Cave and Simonetta (1991) argued for relationships among tardigrades, onychophorans, arthropods, and fossil anomalocarids and "armored lobopods." Bergström (1986, 1987, 1991) and Chen et al. (1994) sug-

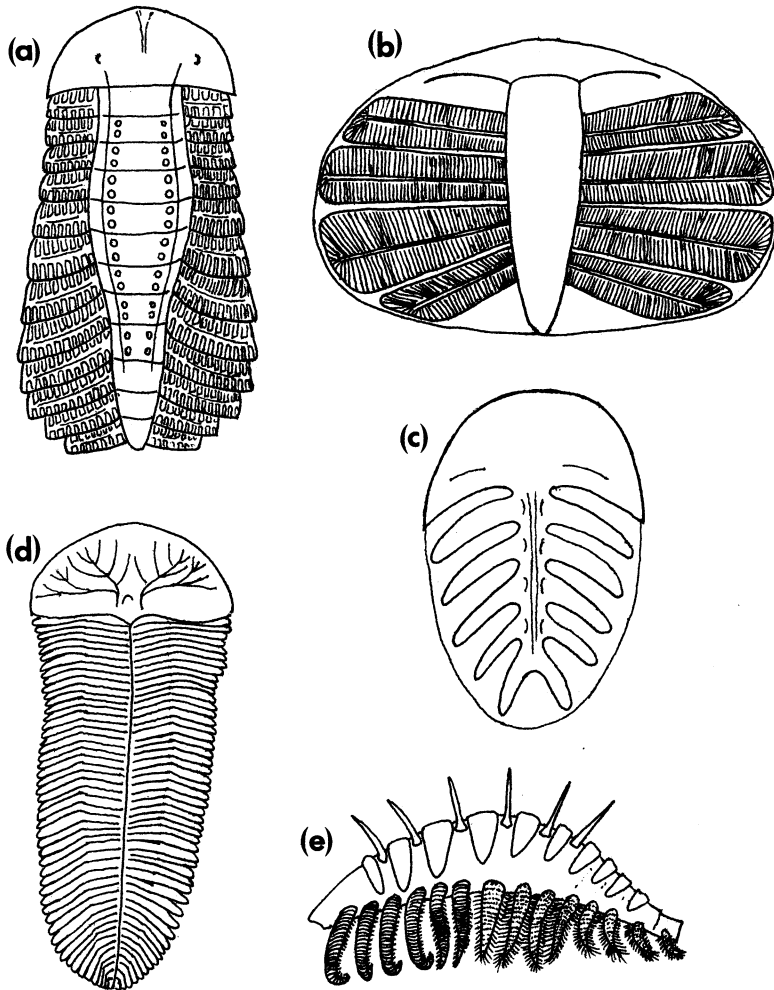


FIGURE 1. Reconstructions of some less well-known taxa used in this analysis. (a) *Bomakellia* (Vendian, Summer Coast, White Sea, Russia), based on Paleontological Institute, Moscow (PIN) holotype 3992/508. Estimated total length, 95 mm; maximum head width, 30 mm. Exact number of segments and reconstruction of terminal four segments is conjectural. (b) *Mialsema* (Vendian, Winter Coast, White Sea, Russia), based on PIN holotype 3993/401. Maximum width, 54 mm. Head reconstruction is conjectural (see note to character 22, Appendix 2). (c) *Vendia* (Vendian, Yarensk borehole, Arkhangel'sk region, Russia), based on the PIN holotype (see Fedonkin, 1985b: pl. 21, fig. 1). Total length, 14 mm. (d) *Marywadea* (Vendian, Ediacara Hills, Australia), based largely on information from Gehling (1991: pl. 4, fig. 1). Total length, 38 mm. (e) "C-monster" (Middle Cambrian, Burgess Shale, British Columbia, Canada) after Delle Cave and Simonetta (1991: fig. 32c).

gested links between the anomalocarids and *Opabinia* (see Briggs and Whittington, 1987, for a dissenting opinion). Dzik and Krumbiegel (1989), Schram (1991), Conway Morris (1993b), and Chen et al. (1994) placed anomalocarids in or very near the arthropods. Valentine (1989, 1991) and Dzik and Krumbiegel (1989) considered

Spriggina to be an early offshoot of the line leading to arthropods, and Gehling (1991) presented evidence that *Spriggina* and *Praecambridium* are arthropod relatives.

Some authors have claimed that lobopod organisms were independently derived from mollusclike coelomate ancestors and are not close to the arthropods (e.g., Hou

and Bergström, 1995, who used *Neopilina* [!] as the outgroup to the lobopods). However, analyses based on both molecules and morphology strongly suggest that onychophorans are close to the arthropods, although opinions differ on their position. Schram (1991) and Ballard et al. (1992) suggested that onychophorans are derived with respect to other arthropod classes, a position they retain in Eernisse et al.'s (1992) reanalysis of Schram's data. However, Ballard et al.'s (1992) 12S ribosomal RNA (rRNA) sequences may not be informative enough for any firm conclusion; at least one onychophoran sequence shows convergence with a chelicerate sequence, and the tree topology is very sensitive to sequence alignment (Wägele and Wetzel, 1994; Wägele and Stanjek, 1995). Lauterbach (1978), Eernisse et al. (1992), and Wheeler et al. (1993) placed onychophorans as sister taxa to the rest of the arthropods, in accordance with a more traditional position.

The aschelminths are a set of pseudocoelomate taxa including the nematodes, gastrotrichs, kinorhynchs, priapulids, rotifers, and others. Some have grouped all these taxa, or most of them, into one phylum (e.g., Hyman, 1951; Bergström, 1989; Nielsen, 1995). Others have stated that the aschelminths are polyphyletic (e.g., Remane, 1963; Willmer, 1990; Ruppert, 1991; Eernisse et al., 1992; Conway Morris, 1993a), a position supported by existing molecular data (Raff et al., 1994). Most phylogenetic hypotheses do not place the aschelminths close to the arthropods. However, preliminary results of an 18S rRNA analysis suggest that the aschelminth taxa do not form a monophyletic clade and appeared early in the metazoan radiation among the protostome phyla (Raff et al., 1994); it is therefore possible that some "aschelminth" groups are sister taxa to the arthropods and their allies. Because this hypothesis is not part of orthodox metazoan phylogenetic thought, a brief review of the evidence for it is presented here.

Tardigrades are usually considered to be arthropod or onychophoran relatives (e.g., Lauterbach, 1978; Kinchin, 1994; Monje-Najera, 1995), but a number of "aschelminth"

features, including ultrastructural features, appear in tardigrades (Dewel et al., 1993; Kinchin, 1994). For example, tardigrades and kinorhynchs both have a ventral ganglia chain with paired connectives, similar sensillae, and tripartite division of the brain (Nielsen, 1995), and the cuticular "pillars" of heterotardigrades are also found in nematodes (Malakhov, 1994). Ruppert (1991) and Kristensen and Higgins (1991) listed a number of features that may link kinorhynchs and arthropods. One priapulid (*Meiopriapulidus fijiensis*) has a system of intraepidermal channels floored by the body wall muscle layer; Störch et al. (1989:330) stated that "a comparable system has not been described from any invertebrate, therefore making interpretation difficult." However, very similar channels are present in living onychophorans (Robison, 1985: fig. 1) and probably existed in fossil lobopods (Robison, 1985; Budd, 1993). Both arthropods and nematodes control the molt cycle with ecdysteroids (Willmer, 1990); onychophorans may also use ecdysteroids, although this use has not been confirmed (Nielsen, 1995).

Several paleontologists have reached similar conclusions regarding an arthropod-aschelminth relationship. Dzik and Krumbiegel (1989) and Dzik (1991, 1993) noted similarities between the fossil lobopod *Xenusion* and the aschelminths and proposed a priapulidlike ancestor for all lobopods, arthropods, and related forms (the details of this hypothesis are examined more critically in Appendix 2). Bergström (1989, 1991) also proposed links among *Anomalocaris*, *Opabinia*, tardigrades, and aschelminths, although he suggested that anomalocarids and tardigrades arose from separate arthropodization events among the aschelminths. In support of these hypotheses, Eernisse et al. (1992) proposed that onychophorans, tardigrades, kinorhynchs, and nematodes are sister taxa to the arthropods in descending order of proximity, with the whole clade in an unresolved trichotomy with priapulids and with the spiralian protostomes. Therefore, two aschelminth taxa—priapulids and kinorhynchs—were included in the present analysis, using priapulids as the

outgroup. These taxa are probably closely related to each other (Lang, 1963; Remane, 1963; Willmer, 1990; Nielsen, 1995). Molecular phylogenetic reconstructions of the animal phyla have not yet included either of these taxa; such an analysis would help to test the hypothesis of an aschelminth–arthropod relationship (Raff et al., 1994).

Annelids have long been considered close to arthropods, or at least to uniramous arthropods (reviewed by Willmer, 1990; Nielsen, 1995), and the Vendian form *Spriggina* has been allied both with annelids and arthropods. However, there is a growing body of evidence that annelids are not close to the arthropods, or at least not their closest relatives (Valentine, 1989, 1991; Delle Cave and Simonetta, 1991; Eernisse et al., 1992; Fryer, 1992; Conway Morris, 1993b; Dzik, 1993; Raff et al., 1994). Schram's (1991) cladistic placement of annelids and pogonophorans as sister taxa to the tardigrade + onychophoran + arthropod clade is at best weakly supported by revisions of his data set (Eernisse et al., 1992; Backeljau et al., 1993; Schram and Ellis, 1994). A different morphological cladistic analysis separates the annelids and arthropods (Eernisse et al., 1992), and new molecular data confirms this separation (Raff et al., 1994; Winnepeninckx et al., 1995; Eernisse, pers. comm.). Therefore, annelids were left out of this analysis.

Dzik and Krumbiegel (1989) and Dzik (1993) proposed relationships between lobopods and Cambrian sclerite-bearing animals such as machaeridians, wiwaxiids, and tommotiids. These animals have usually been compared with either molluscs or annelids (Butterfield, 1990b; Conway Morris and Peel, 1995), but in most cases too little is known about the soft anatomy of these fossils to warrant their inclusion in this analysis. Studies on some exceptionally well-preserved individuals do not obviously suggest a relationship with the lobopods or arthropods (Butterfield, 1990b; Conway Morris and Peel, 1995).

Character Analysis and Scoring

Characters were described, as far as possible, in neutral language; as Beall (1991)

pointed out, this is necessary to avoid preconceived notions of homology from influencing character scoring. All characters were unordered (Fitch parsimony). Analyses were carried out using the ACCTRAN option of PAUP 3.1.1 (Swofford, 1993).

Coding inapplicable characters as missing can lead to impossible ancestral states and unjustified trees (Platnick et al., 1991; Maddison and Maddison, 1992); it is also tantamount to discarding data because characters are coded as if nothing about their state were known, when in fact there is information about their state. However, use of "not applicable" as a separate character state has the effect of decreasing character independence and weighting certain characters very strongly; two taxa that lack a complex structure might be falsely grouped by sharing a large number of "not applicable" character states. This may not be a serious problem in this analysis, because the outgroup, *Priapulius*, has by far the greatest number of not applicable states, which are thus generally made plesiomorphic. In some cases, this problem was avoided simply by coding a morphological feature as one character, absent/present/present with modification, rather than as two characters, absent/present and not applicable/simple/modification. However, the question of how to score inapplicable character states remains a very real problem for this analysis, one for which there is no definitive answer. To examine the effect of both scoring conventions, I analyzed two versions of the data matrix. In the first version (Appendix 3), when a given character described something that was not applicable to a taxon, the nonapplicable character state was scored as 0. Characters were only scored as missing (?) if their state could not be determined from the available material. In the second version (Appendix 4), inapplicable characters were scored as missing, following previous cladistic hypotheses of Cambrian arthropod phylogeny (Briggs and Fortey, 1992; Briggs et al., 1992; Wills et al., 1994).

Two exceptions were made to these scoring conventions. The monuran *Dasyleptus* lacked paired caudal cirri, and the tardi-

grade *Echiniscus* lacks paired sternites. Both of these characters were scored as missing for these taxa because several close relatives of these genera are known to have these features (Carpenter, 1992; Kinchin, 1994). These genera might not be the most representative exemplars of their clades, but they are much better known morphologically than are their relatives.

Hennig's Auxiliary Principle states that convergence should never be assumed; one should always assume homology in the absence of contrary evidence. Ideally, homology has three components: morphological and positional similarity, descent from a common ancestor, and similarity in developmental pathways or developmental constraints (Hall, 1992). Not all of these components are congruent or equally applicable when actually determining homology (Hall, 1992), and the second cannot be used a priori because it is what the cladistic analysis is set up to test. Some developmental information can be obtained from fossils when there are growth series, but for most of the fossil taxa included here there is little or no developmental information (but see Jacobs, 1992); the developmental genetics of living kinorhynchs and tardigrades are also poorly known. Thus, position and gross morphological similarity were used as criteria for evaluating homology. A number of characters whose homology could only be confirmed by careful developmental study and/or much more fossil material, such as precise tagmosis patterns, were also left out (for more extensive character analysis, see Appendix 2).

One character that could have been used but was not was bilateral versus glide reflectional symmetry of the body. Previous hypotheses of the relationships of Vendian organisms have attached great importance to this character. In glide reflectional symmetry, right and left halves of an organism are mirror images but are displaced with respect to each other along the plane of symmetry; there may or may not be unequal numbers of seriated structures on either side. This symmetry is said to be characteristic of Vendian organisms, although some Vendian fossils (e.g., *Bomakel-*

lia and *Mialsemia*) are definitely bilateral. Some authors have claimed that this feature rules out an arthropod affinity, or for that matter a metazoan affinity, for the Vendian fossils (e.g., Bergström, 1991). However, glide reflectional symmetry can also result from distortion or shrinkage (Gehling, 1991; Jenkins, 1992). Despite Bergström's claim that "the alternation of 'segments' of the two sides cannot have so arisen" (Bergström, 1991:27), anomalocarids from Utah (Robison, 1991: fig. 10.3) and the Burgess Shale (Whittington and Briggs, 1985: pl. 10, figs. 44, 45, 47), some Burgess Shale polychaetes (Gehling, 1991), and a possible polychaete from the Devonian Hunsrück Slate of western Germany (Stürmer et al., 1980: pl. 17, fig. 37) all appear to show glide reflection symmetry, sometimes with unequal numbers of appendages on either side, if interpreted literally. Even if glide reflectional symmetry were truly present in Vendian organisms, it would not necessarily separate them from the bilaterian metazoa. Aside from many colonial and sessile metazoans, nudibranchs such as *Tethys*, *Melibe*, and *Tritonia* (Hyman, 1967: figs. 163G, 215B; Beklemishev, 1969: fig. 97E), the tapeworm *Tatria* (Beklemishev, 1969: fig. 93G), a few pelagic polychaetes such as *Travisiopsis* (Fauchald, 1977: fig. 27B), and cephalochordates and agnathans (Simonetta and Insom, 1993: figs. 6A, 6B) all show glide reflectional symmetry, or a variant of it, in a major aspect of gross anatomy. *Peripatus* may show unequal numbers of appendages on the two sides of the body as a rare variant (Lavallard and Campiglia, 1973). Among fossils, certain palaeoscolecids (e.g., Brock and Cooper, 1993: figs. 9-5, 9-8, 9-12) and machaeridians (e.g., Dzik, 1993: figs. 8C, 8E) show glide reflection symmetry in the sclerotome, yet there is no serious doubt that these creatures are metazoans; palaeoscolecids may be close relatives of the "aschelminth" priapulids or nematomorphs (Conway Morris, 1993b; Dzik, 1993; Hou and Bergström, 1994). True glide reflectional symmetry probably appeared more than once among the metazoans, in various structures and organ systems.

Other characters that supposedly sepa-

rate the Vendian fossils from the metazoans are probably not synapomorphies and have no phylogenetic meaning (see Gehling [1991] and Waggoner [1995] for more complete critiques). Seilacher (1989) made the supposed "quilted pneu" morphology of the Vendian fossils the cornerstone of his argument for excluding them from the Metazoa. If a quilted pneu is defined as a fluid-filled sac divided by partitions, then any organism with extensive internal fluid-filled spaces can be considered "quilted": archaeocyathids and sponges, some anthozoans, chondrophorines, annelids, ammonoids and nautiloids, many echinoids, large foraminiferans, and some algae. Furthermore, on a number of Vendian fossils, such as *Vendia*, *Parvancorina*, and *Mialsemia*, it takes imagination to see anything like Seilacher's "fractal and serial quilting." Seilacher's statement that the "vendobiontans" lacked a mouth is contradicted by the presence of branching structures in the anterior end of *Marywadea* and *Praecambridium*; it is difficult to see these as anything other than digestive caecae similar to those found in a number of arthropods (Gehling, 1991). Seilacher (1989) and Bergström (1991) suggested that the arthropodlike Vendian fossils are sessile frondlike organisms in which the "head" is actually the holdfast. However, at least at the Vendian localities on the Winter Coast of the White Sea in Russia, holdfasts of frondlike organisms are often preserved on different bedding planes from their fronds (pers. obs. 1993). I have never seen *Spriggina*, *Vendia*, *Parvancorina*, or any such forms "head in the sand," and I know of no reports of this in the literature or from colleagues.

Search Procedures and Tests of Robustness

The data matrix was analyzed using PAUP 3.1.1 (Swofford, 1993). This matrix is much too large for practical analysis by exhaustive or branch-and-bound search algorithms. Twenty replicates of random addition heuristic searches, using the "steepest descent" option in PAUP 3.1.1, were used to find the most-parsimonious trees. *Priapululus* was used as the outgroup.

To test tree robustness, when a consensus

tree was attained, characters were reweighted according to the maximum value of the rescaled consistency index ($RCI = \text{consistency index [CI]} \times \text{retention index [RI]}$), and the most-parsimonious trees were sought again; this procedure was repeated until tree topology did not change. Tree stability was tested with a measure variously called Bremer support, decay analysis, and length difference (Bremer, 1994). A clade was considered supported if it was found in the strict consensus tree of all trees one step longer than the most-parsimonious trees, all trees two steps longer, and so on, to the limits of available computer memory. These values were used to calculate the total support index as outlined by Bremer (1994). The consistency of this data set with previously proposed hypotheses of arthropod relationships was examined by moving branches of the most-parsimonious trees to new nodes and then searching above and below the nodes for more parsimonious solutions, using MacClade 3.01 (Maddison and Maddison, 1992).

RESULTS

"Not Applicable" Character State

Scored as a separate state.—When inapplicable characters were scored with their own "not applicable" states, two most-parsimonious trees were obtained (Fig. 2), with a length of 515, a CI of 0.324, and an RI of 0.630. Successive reweighting by the best value of the RCI and repeating the search generated nine most-parsimonious trees (Fig. 3) with a CI of 0.416 and an RI of 0.721. The topology of these trees was close to that of the original most-parsimonious trees, but some differences were noted, such as paraphyly of the lobopods. Further reweightings produced the same nine trees.

Bremer support analysis yielded 147 trees of length 516 and 4,279 trees of length 517. Searches for trees of length 518 exhausted available computer memory before terminating. To compensate, the search for trees 518 steps long was repeated three times, using a different random addition sequence each time, and sets of 7,010, 7,509, and 7,136 trees were recovered. Sets of

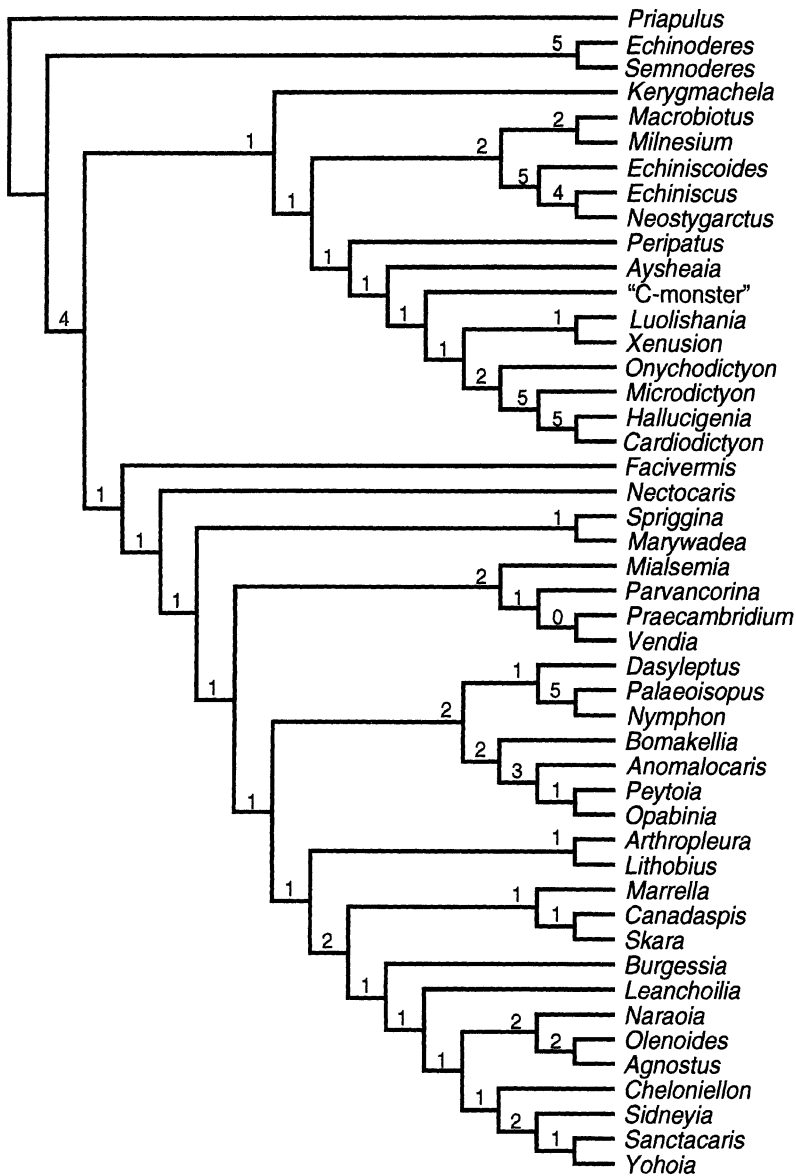


FIGURE 2. One of the two most-parsimonious trees for which inapplicable characters were scored as "not applicable" (length = 515, CI = 0.324, RI = 0.630). Numbers above each branch represent Bremer support index (i.e., the number of additional steps needed to collapse each node to a polytomy).

6,351, 6,427, 6,524, and 6,630 trees 519 steps long were recovered. Only those clades that were supported each time were accepted as being supported at this level. The Bremer support index for the entire tree was 0.157.

Scored as missing.—When inapplicable characters were coded as missing, four most-parsimonious trees were obtained, with a length of 357, a CI of 0.334, and an RI of 0.610 (Fig. 4). Successive reweighting

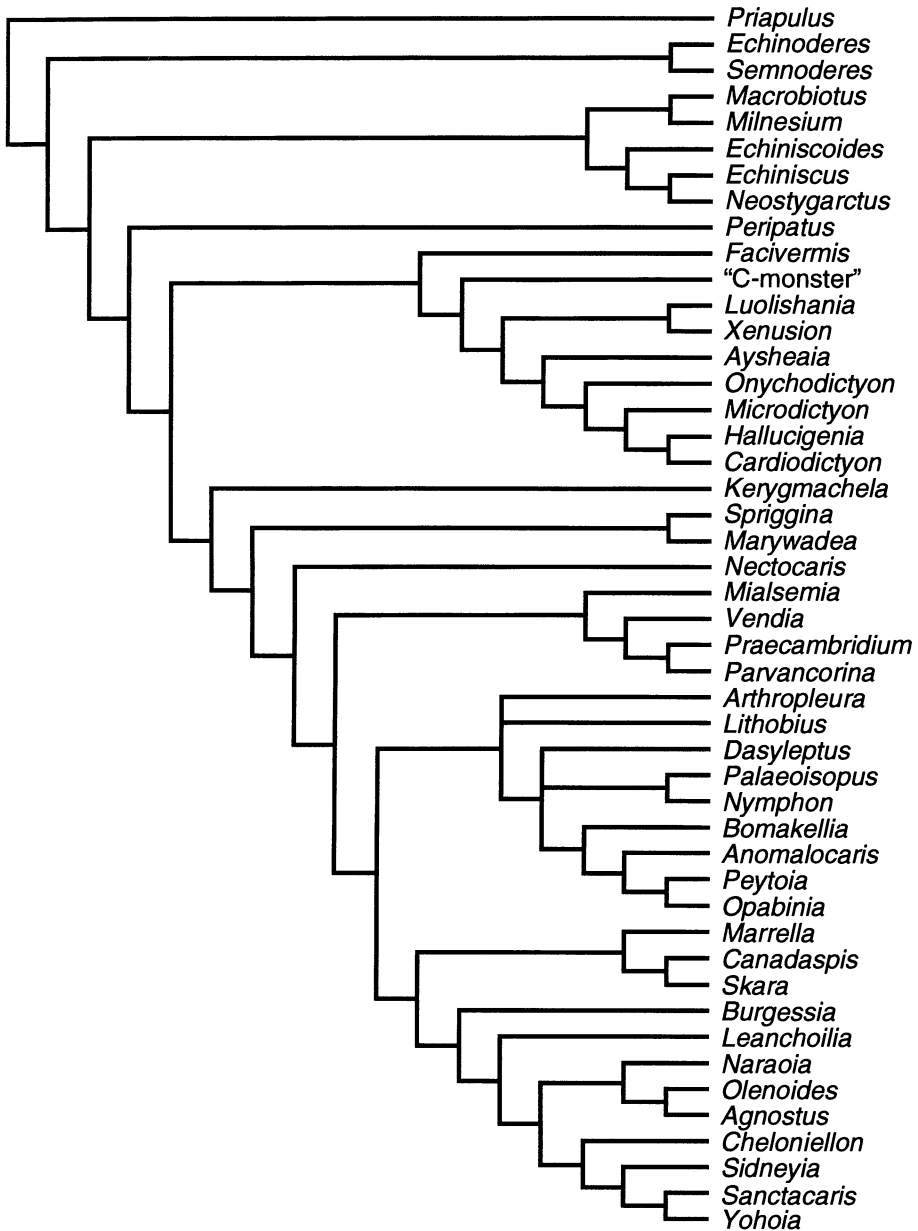


FIGURE 3. Strict consensus of nine most-parsimonious trees found after first reweighting (CI = 0.416, RI = 0.721).

of the matrix by the maximum RCI yielded three most-parsimonious trees, whose topology was unaffected by repeated reweightings. The strict consensus of these trees (Fig. 5) shows some congruence with other searches (e.g., euarthropod monophy-

ly, grouping of trilobitomorphs and "arachnomorph" arthropods) and some taxon placements that are perhaps more "orthodox" than the results of other searches (e.g., *Dasyleptus* grouped with *Lithobius*, *Peripatus* close to the ancestry of euarthropods) but

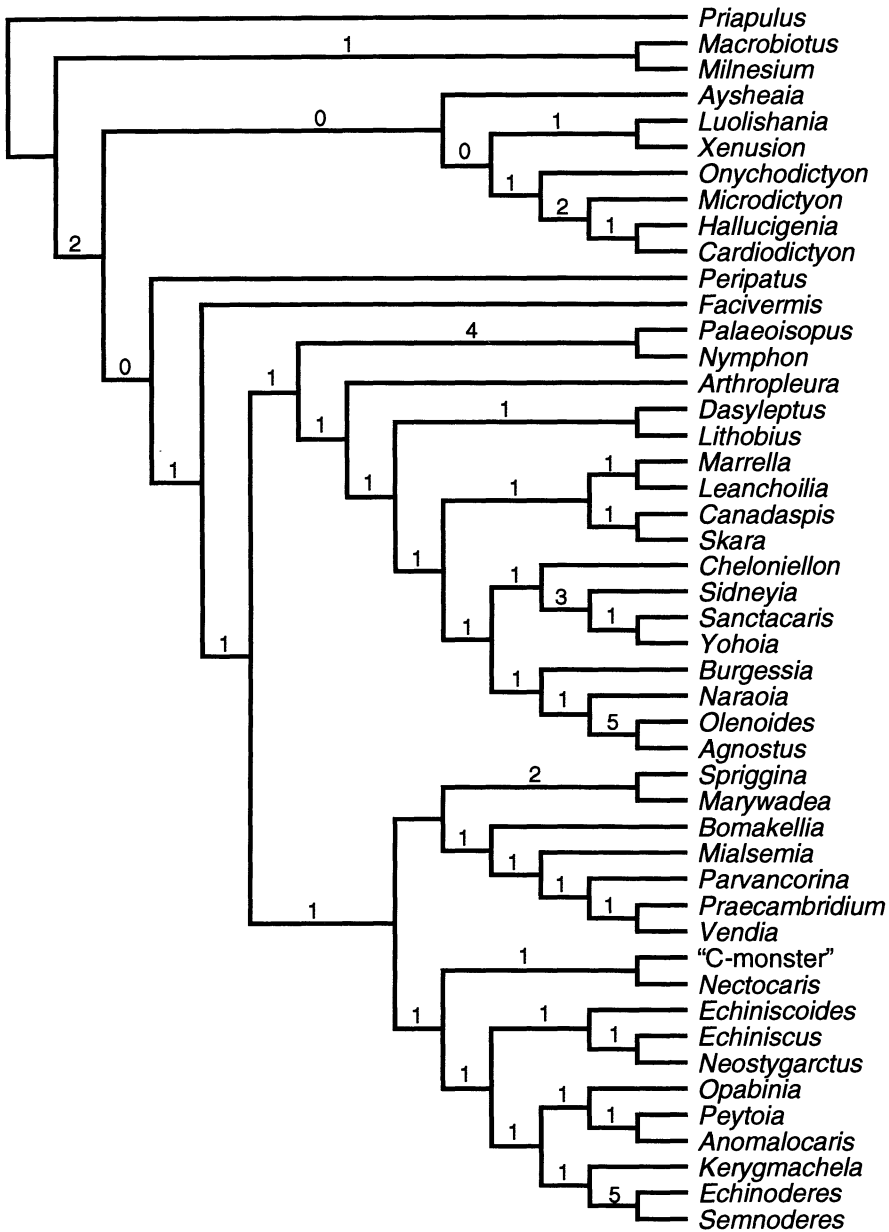


FIGURE 4. One of the four most-parsimonious trees for which inapplicable characters were scored as "missing" (length = 357, CI = 0.334, RI = 0.610). Numbers above each branch represent Bremer support index.

show tardigrade polyphyly, an unusual grouping of heterotardigrades and Vendian forms, and paraphyly of the lobopods. Some of these conclusions are hard to substantiate from more detailed analysis of extant taxa. Two successive reweightings gave

three most-parsimonious trees, which were unchanged in further reweightings. Unlike the first analysis, the topology of the reweighted trees was quite different from that of the original tree (Fig. 6).

As in the first analysis, memory limita-

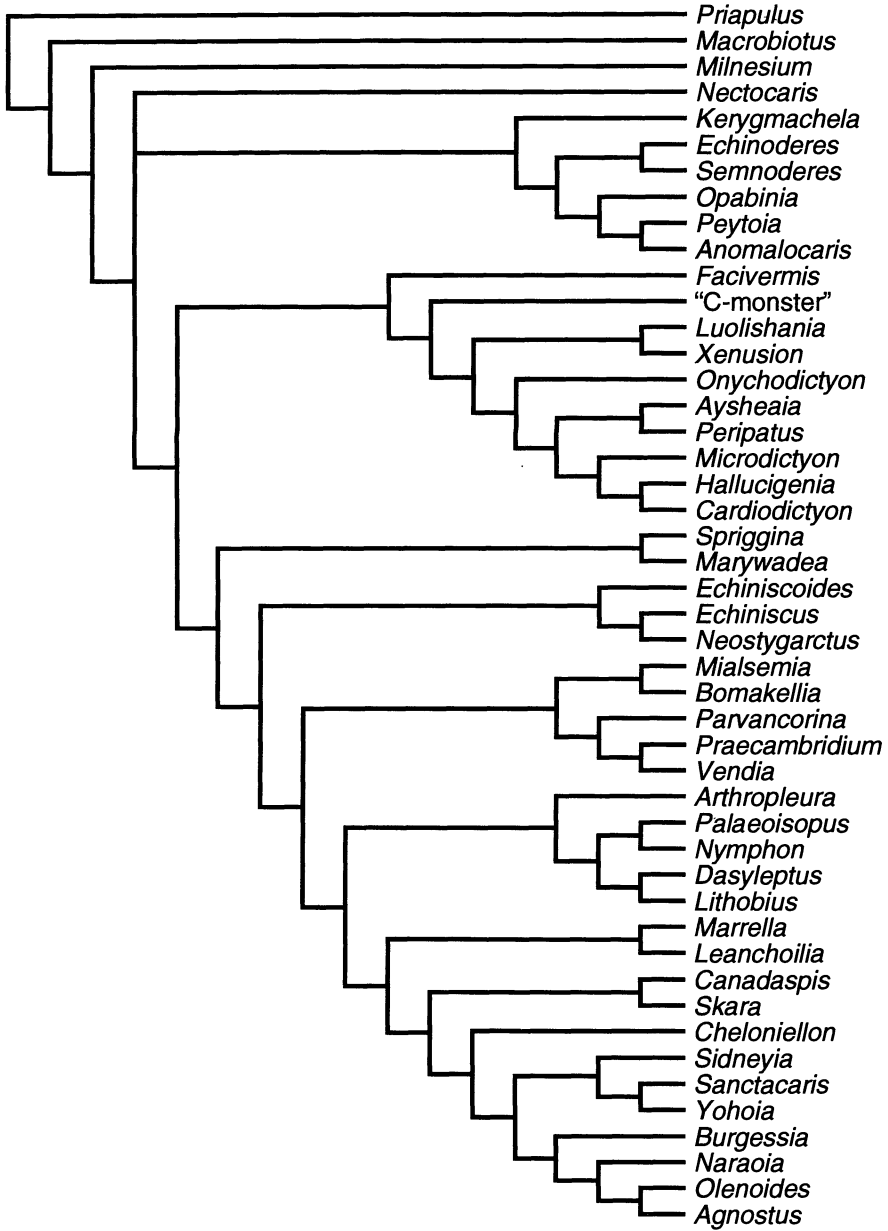


FIGURE 5. Strict consensus of three most-parsimonious trees found after second reweighting (CI = 0.444, RI = 0.738).

tions prohibited full assessment of Bremer support. There were 749 trees of length 358, one step longer than the most-parsimonious trees. Repeated searches with different random addition sequences each time found sets of 7,256, 7,439, and 7,451 trees

of length 359, sets of 6,925, 7,145, and 7,191 trees of length 360, and sets of 6,046, 6,545, 6,832, and 7,165 trees of length 361. The Bremer support index for the entire tree was 0.157.

Comparison of scoring conventions.—Several

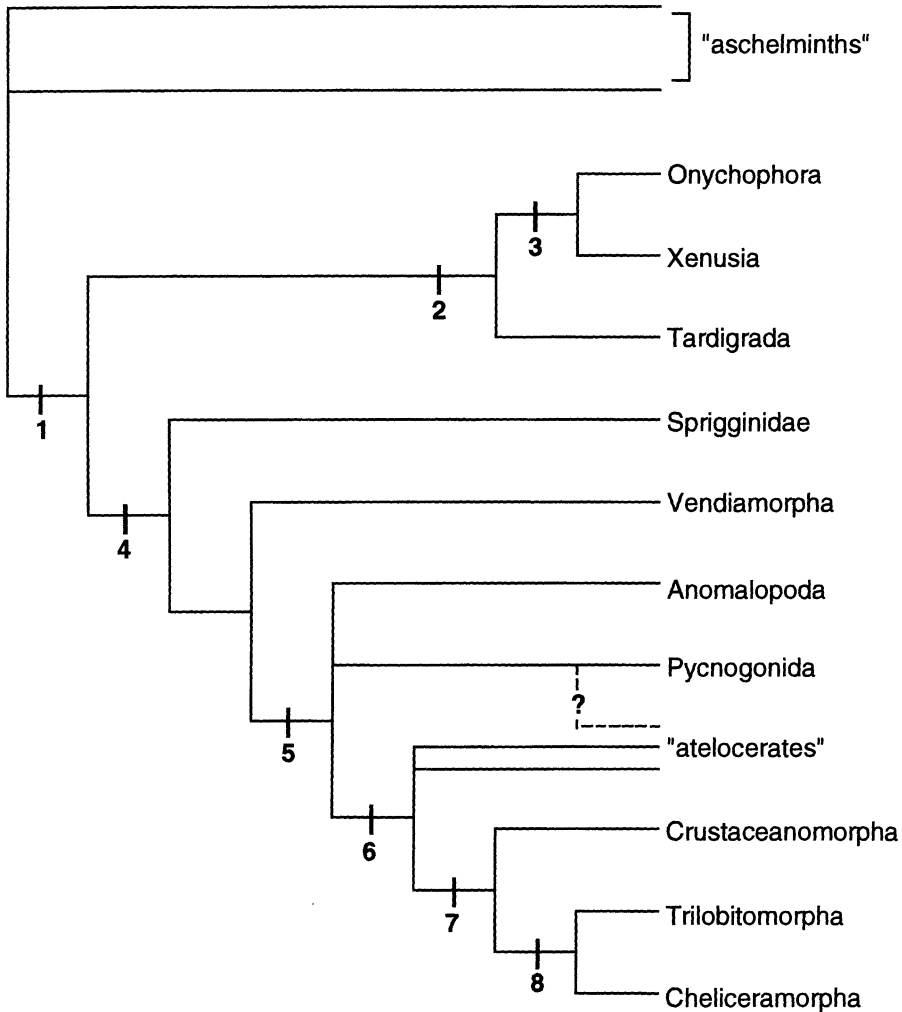


FIGURE 6. Graphic description of taxonomic scheme proposed in this paper. Numbers denote named taxa: 1 = Podophora; 2 = Lobopoda; 3 = Polylobopoda; 4 = Cephalata; 5 = Arthropoda; 6 = Euarthropoda; 7 = Schizoramia; 8 = Arachnomorpha.

clades were supported in both analyses. In both, the arthropods appear monophyletic with clades of "crustaceanomorph" and "arachnomorph" biramous arthropods. The armored lobopods (*Scleronychophora* of Hou and Bergström, 1995), the Cambrian clade of *Sidneyia*, *Sanctacaris*, and *Yohoia*, the trilobites plus *Naraoia*, the pycnogonids, and the "vendiamorph" clade of *Mialsemia*, *Parvancorina*, *Praecambridium*, and *Vendia* are supported by both analyses.

However, in the second analysis, unusual placements of some taxa were noted. The tardigrades appear polyphyletic, with the eutardigrades near the base of the tree and the heterotardigrades highly derived. The kinorhynchs did not appear close to the priapulids but were closer to the anomalocarids. These results run counter to current understanding of morphology; although heterotardigrades and eutardigrades differ in many respects, they share so many characters (similar stylet appara-

tus, fixed number of appendages, pharyngeal bulb with placoids, etc.) that there seems to be no reason to doubt tardigrade monophyly or to group heterotardigrades with anomalocarids and kinorhynchs (Dewel et al., 1993; Kinchin, 1994). There is also abundant morphological and ultrastructural data to support a close relationship between priapulids and kinorhynchs (e.g., Kristensen and Higgins, 1991; Nebelsick, 1993); therefore, the wide separation between priapulids and kinorhynchs renders this analysis suspect. A look at PAUP's reconstruction of character evolution for the second matrix shows that some of these suspect topologies are based on character reconstructions that contradict each other. For example, PAUP internally reconstructed the kinorhynchs as having had only flaplike appendages with venation but also with numerous annulations on lobopods, simple hook-shaped claws, and a single row of appendage spines. The alleged synapomorphies for the clade of *Kerygmachela* + kinorhynchs include the loss of reversal of terminal appendages, which cannot be applied to kinorhynchs. The synapomorphies for this clade + anomalopods include flaplike limbs and one pair of cephalic appendages, which again cannot apply to the kinorhynchs.

For these reasons, I have chosen to use the results of the first analysis as the basis for the following discussion of evolution and systematics. However, in some cases the second analysis yielded results that seem more consistent with external evidence (e.g., relationships within the arthropod clade). Neither method of character scoring is completely satisfactory; the first can effectively weight certain characters very heavily, which may be inappropriate or unintended by the investigator, and the second can lead to inaccurate and contradictory character state reconstructions.

Other measures of support.—Klassen et al. (1991) showed that to be phylogenetically informative a data set must exceed the expected CI for a random data set of the same size, given by the formula $CI_{\text{random}} = 2.9370 \times n^{-0.9339}$, where n is the number of

taxa. For 47 taxa, $CI_{\text{random}} = 0.0806$; I conclude that both data sets are informative.

Sanderson and Donoghue (1989) noted that the CI of a cladogram directly varies with the number of taxa; they empirically derived the formula $CI_{\text{expected}} = 0.90 - 0.022n + 0.000213n^2$ for this relationship. The expected CI for a tree of 47 taxa is 0.337, very close to the actual CI values of 0.322 and 0.334. There has been debate over whether cladograms of Cambrian organisms are less consistent than cladograms of Recent taxa (e.g., McShea, 1993). In the few analyses that have been done, Cambrian organisms are no more prone to homoplasy than are extant organisms (Willis et al., 1994). At present, this is also true for the few cladograms that include Vendian taxa; CI values for cladograms of Vendian and Cambrian frondlike organisms are also well within the range for cladograms of extant taxa (unpubl.). Simonetta's (1990) hypothesis and Gould's (1989) latent genetic potential hypothesis are not supported; homoplasy does not seem more common among Vendian than among Recent taxa. Sanderson and Donoghue (1989) pointed out that unknown character states will tend to increase the CI relative to an analysis in which all characters are known; my analysis clearly showed this effect.

Bremer's total support index (Bremer, 1994) is identical in both analyses. These values are low compared with those given by Bremer (Bremer, 1994), but several clades in each analysis are well supported despite low Bremer support for the entire trees. Because time and memory restrictions kept me from carrying the Bremer analysis to its conclusion (i.e., to the number of extra steps at which the strict consensus tree becomes a complete polytomy), some clades may have higher Bremer support values, and thus the total support indices may be slight underestimates of the true values. This tendency may be counterbalanced by the fact that only subsets of the sets of less parsimonious trees were examined, whose consensus may have supported clades not supported by the full sets of trees.

Tree Topology and Major Clades

Arthropods and anomalopods.—My analysis did not include as many arthropod taxa as have recent analyses of the arthropods alone (e.g., Wills et al. 1994), but it did include some Devonian and Carboniferous taxa that these previous analyses did not include. A number of potentially important characters for inferring arthropod phylogeny, such as differentiation of specific somites and tagmosis patterns, were also left out of my analysis; scoring such characters for the nonarthropod problematic taxa would have mostly been guesswork. Thus, the phylogenies generated by this analysis may not be comparable with the results of other workers.

In the final cladogram, the living arthropods are in a monophyletic group, in agreement with Lauterbach (1978), Turbeville et al. (1991), Field (in Erwin, 1991: fig. 1b), Eernisse et al. (1992), Wheeler et al. (1993), Raff et al. (1994), and Nielsen (1995). There is support for the separation of the uniramian arthropods from the rest of the arthropods (Manton and Anderson, 1979; Willmer, 1990; Anderson, 1993; Budd, 1993) but in an unexpected way: a clade consisting of Precambrian and Cambrian organisms with flaplike appendages, referred to here as anomalopods, comes between some or all uniramous arthropods and the schizoramians. If this placement is correct, the anomalocarids should be placed in the arthropod crown group. However, making the anomalopods the sister taxon of all arthropods, forcing monophyly of the Arthropoda as typically defined, requires only two additional steps. Schram's (1991) placement of *Anomalocaris* as sister taxon to the Crustacea is not supported. The Vendian *Bomakellia* is an anomalopod; this results adds the anomalopods to the lineages that cross the Precambrian–Cambrian boundary.

The branching order within the arthropods closely agrees with that of Wills et al. (1994). Uniramous arthropods are primitive with respect to the Schizoramia, which in turn is divided into crustaceanomorph and arachnomorph clades (equivalent to

the trilobite–crustacean–chelicerate hypothesis). *Marrella* is the most primitive crustaceanomorph, as proposed by Willis et al. (1994). The trilobites and *Naraoia* form a single clade within the arachnomorphs, in agreement with Wheeler et al. (1993), Fortey and Theron (1994), and Willis et al. (1994); Bergström's (1992) placement of the agnostids close to the crustaceans requires at least 14 additional steps. The other main arachnomorph clade is formed by *Sidneyia*, *Yohoia*, and *Sanctacaris*; *Leanchoilia* and *Burgessia* are sister taxa to these two clades, as they are in Wills et al.'s (1994) tree. The Devonian *Cheloniellon* is also an arachnomorph, as suggested by Bergström (1992). The derivation of *Yohoia* directly from an anomalocarid ancestor (Bousfield, 1995) is not supported; this topology required at least 13 extra steps.

The position of the pycnogonids is curious. Wheeler et al. (1993) presented a combined molecular analysis (18S ribosomal DNA and ubiquitin) that grouped their pycnogonid exemplar with the other chelicerates; however, successive weighting placed the pycnogonid at the base of the arthropods. My results agree with those of other workers and with other lines of evidence in placing the pycnogonids outside the arachnomorphs, in a primitive position (e.g., Hedgpeth, 1955; Dzik and Krumbiegel, 1989; Fahrenbach, 1994). In my analysis, placing the pycnogonids anywhere in the arachnomorph clade required at least 11 additional steps. The grouping of pycnogonids with anomalopods seems unusual and was not supported in the second analysis. However, Sharov (1966) proposed a relationship between pycnogonids and *Opabinia*, which he united in the Proboscifera. Although his reconstruction of *Opabinia* was very inaccurate, his hypothesis of relationship may have to be reexamined. More recently, Dzik and Krumbiegel (1989) and Dzik (1993) suggested a link between pycnogonids and anomalocarids. Eye arrangement in pycnogonids and *Opabinia*, radially arranged mouthparts, and possibly raptorial appendages might link anomalopods and pycnogonids; however, fossil pycnogonids are so rare and extant

pycnogonids are so strange that this relationship cannot be strongly supported yet.

A relationship between pycnogonids and insects (represented by *Dasyleptus*) seems even more unusual; making *Dasyleptus* the sister taxon of *Lithobius* (which would be sanctioned by most conventional hypotheses) requires four additional steps. However, in the first analysis, two of the supporting character states are losses (of genal spines and abdominal appendages). The trees based on reweighted characters group all the uniramous arthropods, including the pycnogonids, with the anomalopods but do not resolve their relationships unanimously. In light of suggestions that insects are in fact primitively biramous (e.g., Kukalová-Peck, 1991), I tried recoding *Dasyleptus* as having appendages with a lost exopod, rather than an absent one (character 4). This recoding resulted in reduced overall resolution, but *Dasyleptus* did not shift from its position as sister taxon to the pycnogonids. The analysis with inapplicable characters scored as missing grouped *Dasyleptus* with *Lithobius*, a much more orthodox position.

The phylogenies proposed by Turbeville et al. (1991), Ballard et al. (1992), Winnepeninckx et al. (1992), Wheeler et al. (1993), Averof and Akam (1995), and Bousfield (1995) placed the crustaceans and some or all uniramous arthropods in a monophyletic clade, the Mandibulata. My analysis does not support this arrangement. This group is at best paraphyletic; monophyly of the Mandibulata requires at least six additional steps. Some of these molecular phylogenies, notably those of Ballard et al. (1992), have been criticized by Wägele and Wetzel (1994), who have argued that molecular data alone are insufficient to resolve arthropod relationships. However, the pre-Silurian history of uniramous arthropods (other than anomalocarids) is very poorly known, with only one fossil (the incomplete and poorly known *Cambropodus*) indicating the presence of uniramous arthropods in the Cambrian (Delle Cave and Simonetta, 1991). My results could be due to inadequate sampling.

Vendian clades.—With the exception of *Bomakellia*, the Vendian taxa that were included in this cladogram fall into two clades, successive sister taxa to the arthropods + anomalopods. Most of these forms have relatively few tagmata and a shield that extends over the body; this clade is more or less equal to the class Vendiamorpha Fedonkin 1985. Other, less well-known Vendian taxa, such as *Pseudovendia*, *Onega*, and *Vendomia*, probably should also be classified here; all of these forms possess a shield, although in general they are not well enough known for cladistic analysis. *Spriggina* and *Marywadea* form the next sister taxon, equal to the Sprigginidae Glaessner 1958; they lack a head shield that extends over the thorax and have more numerous segments. Making the Sprigginidae the sister taxon to the Vendiamorpha, creating one monophyletic Precambrian proarthropod clade, required one extra step. This placement supports the phylogenetic hypothesis of Valentine (1991), in which the arthropods arose from flattened hemocoelic wormlike forms, comparable to sprigginids and vendiamorphs. However, Bousfield's (1995) identification of *Spriggina* and *Praecambridium* as antennognath arthropods is not substantiated.

Nectocaris appears to represent a specialized, independent offshoot of the arthropodan stem group; successive reweightings do not alter its position substantially. *Facivermis* may also belong here, but its position is not well supported; successive reweightings group it with the lobopods.

Lobopoda.—Monophyly of the Lobopoda (Onychophora + Tardigrada + marine armored lobopods) is supported, although successive weighting in the first analysis yielded a paraphyletic Lobopoda. Although *Kerygmachela* was not interpreted as having had lobopod appendages in this analysis, it still grouped with the lobopods; placing it anywhere in the anomalopods required at least five extra steps. This result calls into question the interpretation by Chen et al. (1994) of *Kerygmachela* as an anomalopod.

Within this clade, the tardigrades form a monophyletic group. The heterotardigrade-eutardigrade dichotomy, with *Echiniscoides*

as the heterotardigrade closest to the split (Kinchin, 1994), is supported. Placing the tardigrades among the arthropods, as proposed by recent molecular work (C. Ribera, pers. comm. 1994), required at least eight additional steps. Placing them as outgroup to the arthropods and making the Lobopoda paraphyletic, as suggested by Monje-Najera (1995), required at least four extra steps. The recent find of a phosphatized tardigrade in the early Cambrian of Siberia shows that the tardigrade lineage had split off at least by the early Cambrian (Müller et al., 1995).

Onychophorans have sometimes been considered uniramian arthropods (e.g., Gould, 1989; Willmer, 1990; Schram, 1991). The trees presented here contradict the findings of these authors and of Ballard et al. (1992) but agree with those of Briggs et al. (1992), Wheeler et al. (1993), Wills et al. (1994), and Monje-Najera (1995) in removing the Onychophora from the arthropods. Enforcing Ballard's 12S rRNA-based hypothesis, which includes extant onychophorans within the arthropods and makes the insects the sister taxon to the crustaceans, required 22 additional steps; when all lobopods were moved into the arthropods, 24 additional steps were required. Enforcing Schram's (1991: fig. 7) hypothesis, which placed onychophorans and tardigrades within the arthropods and also proposed a different arthropod branching order, required at least 30 additional steps. Enforcing Budd's (1993: fig. 4) hypothesis, in which the Cambrian lobopods are polyphyletic within the euarthropod lineages, required 33 additional steps. In other phylogenetic hypotheses, in which the onychophorans are the sister taxon to the arthropods whose most primitive members are myriapods (e.g., Budd, 1993), the Uniramia could still persist as a paraphyletic group. In this analysis, however, onychophorans are not the closest sister taxon to arthropods; such a position required at least four additional steps, depending on the combination of lobopod taxa moved. The Uniramia is polyphyletic.

The branching order of the Cambrian marine armored lobopods closely follows

Ramsköld's (1992) morphocline and polarizes it: Ramsköld's morphocline is *Aysheaia*–*Luolishania*–*Xenusion*–*Onychodictyon*–*Hallucigenia*, *Microdictyon*, *Cardiodictyon*. The relationship between *Hallucigenia* and *Microdictyon* is supported by finds of Lower Cambrian fossil sclerites that combine features of both taxa (Bengtson, 1991). My results indicate that *Hallucigenia*, *Microdictyon*, and *Cardiodictyon* form a clade, in agreement with Hou and Bergström (1995).

Only one terrestrial onychophoran was used in this analysis, but differences between living onychophorans are slight (the two extant families differ largely in ranges of segment numbers and gonopore position), and there is no reason to suspect that the terrestrial Onychophora are not monophyletic. *Peripatus* is probably the only exemplar needed to assess the position of the terrestrial onychophorans. If the topology presented here is correct, it would imply that the lineage leading to terrestrial onychophorans branched off very early and that the Cambrian lobopods so far found are not their direct ancestors. This result contradicts the cladogram of Monje-Najera (1995), which placed *Aysheaia* as the sister taxon to the terrestrial onychophorans. However, Monje-Najera's apomorphies for *Aysheaia* + extant onychophorans are all losses—of the proboscis, trunk spines, and plates. Making *Aysheaia* and *Peripatus* sister taxa required at least two additional steps; enforcing Monje-Najera's topology for the Cambrian lobopods and onychophorans required at least 19 extra steps.

The fossil lobopods do not form a monophyletic clade with the tardigrades, with which they have often been compared; this result supports the hypothesis of Robison (1985) that the marine lobopods and terrestrial onychophorans should be grouped together. However, making the marine armored lobopods the sister taxon to the tardigrades required only one additional step. Because the few fossil terrestrial onychophorans long postdate the Cambrian (Thompson and Jones, 1980; Robison, 1985), direct fossil evidence for the early evolution of the terrestrial onychophorans is lacking; however, further analysis of a wider range

of tardigrade taxa, including the newly discovered Cambrian tardigrade (Müller et al., 1995), will stabilize this part of the phylogeny.

DISCUSSION

Symmetry as a Taxonomic Character

One character that was not included in the original cladogram can be preserved in fossils and may be important: tetradial symmetry of the integument, mouthparts, and/or body wall musculature around the long axis of the gut. The mouthparts of *Anomalocaris* and the placids of kinorhynchs occur in multiples of four (Nebelsick, 1993), as do the scalids on the introvert of larval *Priapulid* (Higgins et al., 1993). The body wall muscles of nematodes and kinorhynchs (Willmer, 1990: figs. 9.1., 9.4, 9.6) and the aboral "nipples" of palaeoscolecids, which may be priapulid relatives (Dzik and Krumbiegel, 1989; Müller and Hinz-Schallreuter, 1993: figs. 3, 11G), are also tetradially arranged. The lorica ridges of some larval priapulids occur in multiples of four (van der Land and Nørrevang, 1985; Störch, 1991: fig. 12; Higgins et al., 1993), and at least one living priapulid has an octoradial foregut (Störch, 1991: fig. 8A). It is possible that tetradial symmetry of mouthparts and integument structures is symplesiomorphic for the lobopods, anomalopods, and their aschelminth relatives and ancestors; it would have been secondarily lost in the arthropods. Dzik and Krumbiegel (1989) suggested that the lobopods are primitively tetradial, so that both legs and dorsal bosses developed from tetradially arranged spined vesicles of a palaeoscolecidanlike worm. In fact, the intermediate they reconstruct is not unlike the Burgess Shale archaeopriapulid *Louisella* (Conway Morris, 1977: fig. 27), which had two longitudinal rows of spines and papillae (although whether these structures were dorsal or ventral and exactly what they might be homologous with is not obvious).

This possible homology should not be accepted without reservations. Tetradiality may occur in different structures of differ-

ent organisms, and it may be hard to say when it is homologous. Many invertebrate bodies or structures are tetradially symmetric about the major axis: scyphozoan and hydrozoan cnidarians, ctenophores, various organ systems of platyhelminths (Beklemishev, 1969: fig. 55, 57A, 57B), the body wall muscles of aplousobranchs (Hyman, 1967: fig. 9C), and the tentacle crowns of sipunculans (Gibbs and Cutler, 1987). Either tetradial symmetry has appeared several times or (less likely) it appeared only once, but it is too widely distributed to be of much use in metazoan phylogenetic reconstruction. The proposed origin of legs from tetradially arranged vesicles on a wormlike ancestor is hard to reconcile with data on arthropod developmental genetics (J. W. Valentine, pers. comm. 1994), and the details of Dzik's (1991, 1993) scenario may not be correct even if his homologies are accurate. Also, the organisms considered in this analysis show other orders of radial symmetry. Adult priapulid scalids are pentaradially arranged (Hyman, 1951), and kinorhynch and tardigrade buccal structures may occur in multiples of three, four, five, or seven (Nebelsick, 1993; Kinchin, 1994). *Aysheaia* seems to have had six papillae radially arranged around the mouth. The pharyngeal muscles of pycnogonids, kinorhynchs, and tardigrades are triradially arranged, as they are in other aschelminths and in leeches; Willmer (1990) noted that this character is prone to homoplasy, representing simply the most efficient way to pack muscles around a sucking pharynx.

Nevertheless, the simple presence of any order of radial symmetry of the gut, mouthparts, and musculature about the major axis may be phylogenetically significant. If this were true, the anomalocarids would go from weird wonders to missing links, combining aschelminth characters (radially arranged spinose or platelike oral structures) with arthropod characters (jointed appendages). However, whether this state is plesiomorphic for the taxa included here or was derived independently in the anomalocarids is not known, because the mouthparts and gut of the Vendian taxa are not

known. Work on development of living organisms with this kind of symmetry would be useful for evaluating whether radial symmetry is homologous, how it may have appeared, and how plastic the degree of radial symmetry may be.

*Trace Fossils and the Evolution of
Organism Size*

One objection to placing Vendian body fossils with the metazoan bilaterians is the lack of any trace fossils that correspond to known body fossil taxa. However, anomalopods may have spent much of their time swimming, as has been inferred for *Anomalocaris*, and the only traces they would normally leave would be resting traces. *Vendichnus vendicus*, from the Summer Coast of the White Sea, may represent such a trace (Fedonkin, 1985c: pl. 19, fig. 10); it has also been interpreted as the resting mark of a nektonic arthropod. Many Vendian bilateral metazoa may have made small and nondescript trace fossils: for instance, collections of round fecal pellets are common in the Vendian (Fedonkin, 1985c; pers. obs. 1993) and could have been made by known Vendian bilaterians. Scratch marks attributable to arthropodlike organisms have been found in Australia (Gehling, 1991: pl. 6, fig. 3) and possibly in north Russia (pers. obs.).

However, more distant ancestors of the arthropods may have been meiofauna that left no identifiable traces at all (Conway Morris, 1993a). Dzik (1991, 1993) derived arthropods (and most other metazoan phyla) from priapulid ancestors, stating that "transitions between phyla took place at the level of relatively large, hydraulically propelled animals" (Dzik, 1991:54). However, over half of all living priapulid species, which show most of the morphological diversity in the taxon, are meiofaunal and nearly microscopic (van der Land and Nørrevang, 1985), as are all kinorhynchs and tardigrades. If size is phylogenetically meaningful, then the cladogram presented here supports a hypothesis opposite to Dzik's (1991, 1993) scenario: ancestors are likely to have been small, with large size the derived state, probably attained several times independently. This hypothesis is

hard to test because there are very few unquestionable meiofaunal-size body fossils of Precambrian and Cambrian animals (but see Müller et al., 1995). However, a few Precambrian microfossils, fecal pellets, and bioturbation structures tentatively suggest that the earliest metazoans, perhaps including the ancestors of the arthropods and their kin, were meiofaunal (reviewed by Fedonkin, 1992; Conway Morris, 1993b). This hypothesis needs much more documentation and testing.

SYSTEMATICS

If the Onychophora and Tardigrada are to be included in the Arthropoda, as some systematists have proposed, then all of the taxa examined here, except for the kinorhynchs and priapulids, should be considered arthropods. This arrangement would involve a rather drastic redefinition of the concept of the Arthropoda. However, if the name Arthropoda is restricted to roughly its traditional sense, several high-level clades outside of the Arthropoda can be named. These clades could be designated superphyla, phyla, or subphyla within the Linnean system. However, the use of unranked names (de Queiroz and Gauthier, 1992) probably is the best way to work with the phylogeny of weird wonders and high-level clades. Smith (1994) argued for the retention of Linnean rank for ease of communication among systematists. However, the use of unranked high-level taxa is already routine in discussions of metazoan systematics; Eumetazoa, Bilateria, Deuterostomia, Protostomia, Articulata, Spiralia, Eutrochozoa, Lophophorata, and others are in common use.

I propose the name Podophora ("leg bearers") for all organisms included in this analysis, except the kinorhynchs and priapulids, and all of their living and fossil relatives. My classification of the Podophora is outlined in Figure 6, and brief diagnoses are given below († = extinct clade).

I. Cephalata nom. nov. (Vendian–Recent) typically have a seriated body, narrow appendages, and a definite head area, which in many forms is enlarged and broad.

They share plesiomorphies (chitinous multilayered cuticle, molting controlled by ecdysteroids, etc.) with various "aschelminth" taxa.

A. Arthropoda Siebold and Stannius 1848 (Vendian–Recent) is the crown clade of the Cephalata. It includes euarthropods and anomalopods.

1. Euarthropoda Lauterbach 1978 (?Vendian, Cambrian–Recent) includes those organisms classically considered true arthropods, i.e., trilobites, chelicerates, crustaceans, etc., with jointed limbs and segmented cuticle. This clade appears in the early Cambrian, but some Vendian fossils (scratch marks and "soft-bodied trilobites") may also represent euarthropods or their stem lineage. The arthropods with uniramous appendages, excluding the pycnogonids, were paraphyletic in every analysis. Remaining arthropods form a monophyletic Schizoramia, which is split into the Crustaceanomorpha (crustaceans and various Cambrian taxa) and the Arachnomorpha (trilobites, chelicerates, and various Cambrian taxa). However, other analyses have supported monophyly of the crustaceans + atelocerates in a clade often called the Mandibulata; more work is needed to resolve atelocerate relationships.

2. †Anomalopoda nom. nov. (Vendian–Cambrian) includes the Cambrian *Anomalocaris*, *Peytoia*, and *Opabinia* and the Vendian form *Bomakellia* and all of their relatives. Anomalopods have laterally extending flaplike appendages with venation or folding, and those whose mouthparts are known had radially arranged plates surrounding the mouth and enlarged uniramous raptorial appendages. Cambrian anomalopods are inferred to have been nektonic predators. In the absence of preserved mouthparts in the only Vendian anomalopod, it is not known whether Vendian anomalopods were predators or whether they occupied some other trophic niche; their identification as predators would contradict the Garden of Ediacara hypothesis of the Vendian as an idyllic time without predation (McMenamin, 1986; McMenamin and McMenamin, 1990). The possible relationship between the pyc-

nogonids and the anomalopods should be examined further. Pycnogonida is retained as a separate clade for the present.

B. The stem group of the Cephalata includes the clades †Vendiamorpha and †Sprigginida.

1. †Vendiamorpha Fedonkin 1985 (Vendian, ?Cambrian) includes *Praecambridium*, *Parvancorina*, and *Vendia*. The Vendian taxa *Onega*, *Vendomia*, and *Pseudovendia* probably also belong here. This clade is not known to have survived into the Phanerozoic. Simonetta and Insom (1993) discussed *Skania* as a possible survivor from the Middle Cambrian Burgess Shale. *Skania*, however, is very close to the fossils described as *Naraoia* protaspides (Hou et al., 1991) and thus may be a true arthropod.

2. †Sprigginidae Glaessner 1958 (Vendian, ?Cambrian) includes the two genera *Spriggina* and *Marywadea*. Simonetta and Insom (1993) described *Metaspriggina*, a possible Cambrian survivor in this clade. *Metaspriggina* is not well preserved, but it may be an early chordate, based on the position of what may be the digestive tract and anus (Briggs et al., 1994).

3. †*Nectocaris* Conway Morris 1976 (Cambrian) appears to represent another stem lineage of the Cephalata, but its morphology is still not well understood. Perhaps the hypothesis that *Nectocaris* is a chordate (Simonetta, 1988) should be reexamined; until more fossils are found, it will be difficult to place *Nectocaris* definitively. †*Facivermis* (Cambrian) may also be a stem cephalate, but successive reweightings group it with the Lobopoda. It remains *incertae sedis*.

II. Lobopoda Snodgrass 1938 (Cambrian–Recent), the sister taxon to the Cephalata, includes forms with clawed lobopod appendages. It contains two main crown clades.

A. Tardigrada Spallanzani 1777 (Cambrian–Recent) is retained in its usual sense: microscopic organisms with four pairs of clawed lobopods, paired piercing stylets, no mouthparts derived from appendages, capacity for anhydrobiosis in many (but not all) species, etc. My analysis

substantiates the traditional division of the Tardigrada into Heterotardigrada and Eutardigrada.

B. Polylobopoda nom. nov. are larger than the tardigrades, have more than four pairs of appendages, and completely lack anhydrobiosis as far as is known.

1. †Xenusia Dzik and Krumbiegel 1989 (Cambrian) includes marine polylobopods with more or less unspecialized appendages serving as mouthparts. There are several competing hypotheses of relationships within the Xenusia (see Hou and Bergström, 1995; Monje-Najera, 1995), and I am not yet formally proposing any cladistically defined taxa within the Xenusia. However, my results strongly support the monophyly of *Cardiodictyon*, *Hallucigenia*, and *Microdictyon*, which were placed by Hou and Bergström (1995) in the †Scleronychophora.

2. Onychophora Grube 1853 (Pennsylvanian–Recent) is retained to include all terrestrial polylobopods. Apomorphies for this group include antennae, paired mouth papillae associated with slime glands, and paired jaws derived from the third appendages.

C. *Kerygmachela* Budd 1993 appears as the stem group to the Lobopoda. However, the position of this fossil form is not stable, and the position may depend on the scoring convention used in the analysis.

CONCLUSIONS

1. Arthropoda is a monophyletic crown clade; the branching order obtained here is congruent with that of several previous analyses based on morphology and on molecules. Onychophorans, however, are neither arthropods nor their closest sister taxon, and the old grouping of onychophorans and atelocerate arthropods is not supported.
2. *Anomalocaris*, *Peytoia*, and *Opabinia*, though wondrous indeed, are not as "weird" as they have been given credit for being. They share synapomorphies with the rest of the Podophora and can be placed in the clade Anomalopoda within the Arthropoda. Anomalopods are true Ediacaran survivors, closely re-

lated to the Vendian *Bomakellia*. If anomalopods are included in the Arthropoda, as proposed in this paper, then the stratigraphic range of the Arthropoda may be extended into the Precambrian. The Anomalopoda should be included in future analyses of arthropod phylogeny.

3. The cladistic analysis presented here implies that the main podophoran lineages were differentiated by the middle Vendian, a hypothesis that receives some support from Vendian trace fossils. It also questions the Garden of Ediacara hypothesis by suggesting that the Vendian *Bomakellia* is a member of a clade whose Cambrian representatives were formidable predators.
4. There seems to be no compelling reason to consider the sprigginiids and vendiomorphs as unrelated to the main lines of the evolution of metazoan bilaterians.
5. A hypothesized relationship between arthropods and certain "aschelminths" seems to help in interpreting certain features of problematic fossil and living arthropods; this hypothesis merits further study.
6. Problems for future research indicated by this analysis include the relationships of the pycnogonids, interrelationships of the lobopods (in particular monophyly of the Tardigrada), and possible arthropod–aschelminth connections.

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APPENDIX 1

SOURCES FOR TAXONOMIC DESCRIPTIONS, CHARACTER CODING, AND CHARACTER ANALYSIS

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APPENDIX 2 ANNOTATED LIST OF CHARACTERS

1. Appendages: 0 = absent, 1 = present.
Interpretation of the Vendian fossils *Praecambridium*, *Vendia*, and *Parvancorina* is difficult and includes some unavoidable speculation. I interpret the seriated structures visible in these first two taxa as appendages or possibly as gut diverticula that extend into the limbs, as in extant pycnogonids (Fig. 1c). As for *Parvancorina*, it is hard to say whether the “corrugations” on the carapace are appendages or wrinkles on the carapace; reconstructions of the appendages (Glaessner, 1979) were criticized by Bergström (1991). Gehling (1991) mentioned undescribed specimens that seem to show biramous appendages, but these were not obvious in any material I have seen. Although I have followed Glaessner (1979) in reconstructing the appendages of *Parvancorina*, I have not scored them as arthropodlike or as biramous.
2. Freedom of appendages: 0 = not applicable, 1 = all partially free, 2 = last pair partially free, 3 = all completely free.

There has been some debate as to whether *Spriggina* and its relatives had free limbs or not. On the basis of the material I have seen, I opt for a median position. Birket-Smith (1981) proposed that the lateral ridges represent completely free limbs, but I consider this overinterpretation. I also do not believe that these ridges were entirely joined, as “quilting” (Bergström, 1991) or as annelidlike segments. The ridges were largely joined along their length but were free at the tips and formed laterally directed bulges that I have homologized with true limbs (Fig. 1d). The specimen of *Spriggina borealis*,

from the Winter Coast of the White Sea, shows the independence of appendage tips somewhat more clearly than specimens of the Australian *S. floundersi* (Fedonkin, 1985b: pl. 21, fig. 5). Something analogous (not necessarily synapomorphic) may be seen in the posteriormost appendage pairs of *Macrobiotus* and *Milnesium*, which are shortened and partially joined (Kinchin, 1994). Valentine (1991, 1994) and Fryer (1992) have put forth scenarios in which appendages arise from rudimentary outgrowths on segmental margins; Dzik’s (1991) hypothesis is broadly similar in that legs appear from tubercles of a seriated wormlike animal. For now, I do not accept the specific form of Dzik’s hypothesis, that legs are homologous with the paired dorsal bosses of palaeoscolecoid worms and armored lobopods.

3. Limb rami: 0 = not applicable, 1 = uniramous, 2 = biramous.
4. Lamellar rami on anterior biramous appendages: 0 = not applicable, 1 = absent, 2 = lamellar rami present, 3 = reduced to flagella (autapomorphic for *Burgessia*), 4 = lost.
Extant chelicerates are generally interpreted as having secondarily lost the outer rami of the appendages on the prosoma, and I have extended this interpretation to several Cambrian taxa for which it seems plausible.
5. Walking ramus on posterior biramous appendages: 0 = not applicable, 1 = present, 2 = absent.
6. Limb type for all appendages except anteriormost ones: 0 = not applicable, 1 = lobopod, 2 = unjointed and flaplike, 3 = jointed stenopod, “arthropodlike.”
7. Limb type for anterior appendages: 0 = not applicable, 1 = lobopod, 2 = unjointed and flaplike, 3 = jointed, “arthropodlike.”

I homologize all appendages as being derived from an ancestral uniramous “lobopod,” as suggested by the probable position of tardigrades and/or onychophorans as outgroups to the arthropods in other phylogenetic analyses (e.g., Lauterbach, 1978; Eernisse et al., 1992; Wheeler et al., 1993). This lobopod may transform to an arthropodlike jointed limb, probably as a natural result of cuticle thickening, or flatten to a flaplike limb; Dzik and Krumbiegel (1989) gave developmental evidence for this polarity. Flattened appendages could also arise from the endopodite of a primitively biramous limb, the exopodites of which have been lost, as Bergström (1986) suggested. Briggs and Whittington (1987) were critical of this idea, and I have not used it.

Bergström (1986, 1987) also suggested that the “flaps” of *Opabinia* are not appendages but pleural extensions of the dorsal tergites. Briggs and Whittington (1987) and Delle Cave and Simonetta (1991) were dubious, and so am I.

8. Lobopod type: 0 = not applicable, 1 = smooth, 2 = few annulations (“telescoping”), 3 = numerous annulations.

Kinchin (1994) cited earlier work that described the “telescoping” appendages of halechiniscid tardigrades as “arthropodan,” but no systematic con-

clusions were drawn. Nielsen (1995) argued that this feature is a synapomorphy for the tardigrades and euarthropods. The possibility of homology merits further study, but at present I have not scored telescoping heterotardigrade limbs as true arthropod appendages. They seem to be functionally different: they can lengthen and shorten by telescoping, unlike arthropod appendages.

Birket-Smith (1981) proposed that *Spriggina* had annulated lobopodlike legs; this is probably an overinterpretation.

9. Venation of flaplike appendages: 0 = not applicable, 1 = absent, 2 = present.
10. Reversal of terminal appendages: 0 = not applicable, 1 = no reversal, 2 = reversal.
11. Number of pairs of reversed terminal appendages: 0 = not applicable, 1 = terminal pair reversed, 2 = last two pairs reversed, 3 = last three pairs reversed.

Three groups show reversal of the posteriormost appendage(s). Heterotardigrades frequently reverse the last pair, and Cambrian marine lobopods frequently reverse the last pair or two pairs, so that the terminal claws, spines, and other leg structures point in the opposite direction from those on the rest of the appendages. This reversal may aid locomotion (Ramsköld, 1992), but tardigrades live in very different environments at different Reynolds numbers from the Cambrian lobopods, and the function may not be the same in both taxa. *Opabinia* also shows reversal of the appendages forming its tail fan; they imbricate in the opposite direction from the rest of its appendages. *Anomalocaris* is now known to have had a very similar fan (Chen et al., 1994). Bergström (1986, 1987) argued from this that the flaps making up the tail fan were ventral sclerites, presumably not homologous to the flaplike appendages. Briggs and Whittington (1987) did not accept this, and I see no reason to. The presence of terminal appendage reversal in three groups, in which its functions are very different from each other, suggests that terminal appendage reversal is homologous.

12. Well-developed spines on appendages: 0 = not applicable, 1 = absent, 2 = single row, 3 = double row.
13. Number of terminal claws per appendage: 0 = not applicable, 1 = no terminal claws, 2 = one, 3 = two, 4 = four, 5 = more than four.

These terminal elements are not chelae but rather are sclerotized hooklike claws, as seen in tardigrades, onychophorans, and also some arthropods.

14. Terminal claw morphology: 0 = not applicable, 1 = simple hook, 2 = branched hook.
15. Cephalic digestive caecae: 0 = absent, 1 = unbranched and directed along leading edge of headshield (anchor type), 2 = radiate branching, 3 = single blind, unbranched caecum on midline (autapomorphic for *Leancoilia*).

See Gehling (1991) for documentation and analysis of the presence of this character in the Precambrian forms *Praecambridium* and *Maryuadea*.

16. Compound eyes: 0 = absent or simple photoreceptors only, 1 = present.

Dzik (1993) noted the similarity between the dorsal plates of *Microdictyon* and trilobite schizochroal eyes and hypothesized that the two were homologous. Although the dorsal bosses on fossil lobopods may well have had some sensory function, I consider this homology too far-fetched at this stage of knowledge. Birket-Smith (1981) claimed that *Spriggina* had compound eyes, but I consider this to be overinterpretation. For discussion of the homology of arthropod eyes, see Paulus (1979).

17. Number of eyes: 0 = not applicable, 1 = paired, 2 = two pairs.
18. Eyes pedunculate: 0 = not applicable, 1 = apedunculate, 2 = singly pedunculate, 3 = several eyes on tubercle.
19. Median eye: 0 = not applicable, 1 = absent, 2 = present.
20. Eye shape: 0 = not applicable, 1 = round, 2 = crescentiform.
21. Eye location: 0 = not applicable, 1 = on headshield, 2 = below headshield.
22. Definite head or cephalon: 0 = head undefined, 1 = definite head.

M. A. Fedonkin (pers. comm. 1993) informed me that the only specimen of *Mialsemia* had a nondescript crescent-shaped head, which was lost during preparation. Accordingly, I have scored this taxon for a broad head (see Fig. 1b) but refrain from assumptions as to its head structures.

23. Head separated from body by sulcus: 0 = not applicable, 1 = no sulcus, 2 = sulcus.
24. Head shape: 0 = not applicable, 1 = narrow to equilateral, 2 = broad.
25. Glabella: 0 = absent, 1 = present.
26. Cephalic shield: 0 = none or simple head capsule, 1 = shield present.
27. Shield type: 0 = not applicable, 1 = univalved, 2 = bivalved.

Hou and Bergström (1995) showed that *Cardiodictyon* and *Hallucigenia* bore a pair of expanded plates covering the head and first pair of appendages; this has been incorporated into my analysis. Simonetta (1988) suggested that the "carapace" of *Nectocaris* is the peribranchial chamber of a chordate. If this is true, then *Nectocaris* should be removed from this analysis. The only fossil of *Nectocaris* shows no unequivocal gill slits, straight segments instead of "zigzag" myomeres, and large eyes unlike those of early chordates; in my opinion, the evidence for chordate affinities for *Nectocaris* is interesting but not at all conclusive. More fossils of *Nectocaris* will probably be necessary to settle the question.

28. Extent of shield: 0 = not applicable, 1 = restricted to head, 2 = extends back over thorax.
29. Cephalic sutures: 0 = not applicable, 1 = absent, 2 = present.
30. Cephalic doublure: 0 = not applicable, 1 = absent, 2 = present, 3 = anterior tip only turned up (autapomorphic for *Leancoilia*).

31. Genal spines: 0 = not applicable, 1 = absent, 2 = present.
32. Number of pairs of cephalic/anterior appendages: 0, 1, 2, 3, 4, 5.
33. Number of pairs of antenniform appendages: 0, 1, 2.
34. Mouth location: 0 = terminal, 1 = subterminal to ventral.
35. Cephalic limbs morphologically specialized as mouthparts: 0 = not applicable, 1 = no specialization, 2 = gnathobase, 3 = grasping with tip, 4 = fusion into clawed organ (autapomorphic for *Opabinia*), 5 = *Burgessia*-type (autapomorphic for *Burgessia*).
36. Enlargement of mouthparts into raptorial appendages: 0 = not applicable, 1 = no enlargement, 2 = enlargement.
37. Great appendages: 0 = not applicable, 1 = absent, 2 = present.

Bergström (1986, 1987; also Dzik, 1993; Chen et al., 1994) revived and revised an idea that Gould (1989) attributed to Simonetta (1970) and stated that the proboscis of *Opabinia* was derived from a fusion of two appendages (Simonetta [1970] did not explicitly state this). Bergström homologized the proboscis with the paired grasping mouthparts of *Anomalocaris*. This homology has been criticized in the past (Briggs and Whittington, 1987), but the close relationship between *Anomalocaris* and *Opabinia* was supported in an earlier analysis even when the proboscis of *Opabinia* was coded as an autapomorphy, not homologous to appendages. In this light, the proposed homology appears more likely and was scored as such in the final cladogram. However, there is no real reason to suggest that the entire proboscis represents a pair of fused appendages (Gould, 1989); it may be more likely that the proboscis of *Opabinia* represents an elongated preoral body segment whose appendages form the terminal claws (Bousfield, 1995).

The arthropods *Yohoia* and *Leancoilia* also have anterior appendages enlarged into "great appendages," as do several other Cambrian arthropods. Dzik (1993) and Bousfield (1995) suggested that these raptorial appendages are homologous with those of *Anomalocaris*. However, Jacobs (1992) suggested that unusual preoral appendages evolved by ectopic expression of posterior segment genes and thus may have evolved in parallel in a number of lineages. Patterns of gene expression are not easily assessed in fossils with no obvious living analogue; nonetheless, Jacobs's hypothesis should be kept in mind. I did not homologize arthropod great appendages and anomalocarid raptorial appendages. The great appendages of *Yohoia* and *Leancoilia* have elongated extensions of the distal three or four podomeres, which either form a sort of claw, as in *Yohoia*, or are elongated and filiform, probably serving as sensory organs, as in *Leancoilia*. Such extensions are sometimes present in anomalocarid appendages but are longest on the proximal podomeres when present (Bousfield, 1995).

38. Circumoral plates: 0 = absent, 1 = present.

I have proposed homology between the mouth-

parts of *Anomalocaris* and *Peytoia* and aschelminth and tardigrade circumoral structures. The kinorhynch mouth, when retracted, is covered by a circlet of 16 overlapping plates, the placids (Hyman, 1951; Nebelsick, 1993). Anomalocarids had 32 plates of similar shape encircling the mouth. Tardigrades have similar platelike structures, the lamellae, although these are much smaller in relation to body size than the mouthparts of anomalocarids (Kinchin, 1994). Priapulids and kinorhynchs have multiple rows of scalds on the eversible proboscis. Anomalocarids had circlets of serrated teeth inside the pharynx in addition to the large outermost circlet (Whittington and Briggs, 1985); the position and cusps on these internal teeth make them similar to priapulid scalds.

Butterfield (1990a) compared anomalocarid mouthparts with the circumoral plates of the Carboniferous agnathan *Pipiscius* and suggested that the two might be related. I consider this to be convergence. Anomalocarids lack dorsoventral fins, notochord, postanal tail, and gill slits, and their jointed arthropodlike mouthpart appendages have no counterpart in any chordate.

39. Eversible pharynx: 0 = absent, 1 = present.

The mouthparts of anomalocarids could be opened and closed in a manner analogous to that of priapulid and kinorhynch mouthparts (Briggs et al., 1994), although it is not likely that they could be extruded far.

40. Mouth on proboscis that extends well past first appendages: 0 = no proboscis, 1 = proboscis present.
41. Labrum: 0 = absent, 1 = present.
42. Trunk appendages diminishing in size: 0 = not applicable, 1 = not significantly diminishing, 2 = diminishing posteriorward, 3 = diminishing both posteriorward and anteriorward.
43. Appendage attitude: 0 = not applicable, 1 = pendant, 2 = lateral.
44. Number of total tagma/appendages/segments: 0 = none, 1 = four, 2 = 5–10, 3 = 11–15, 4 = 16–20, 5 = more than 20.
45. Oral papillae: 0 = absent, 1 = present.
46. Dorsal cuticle subdivided into serial tergites: 0 = undivided, 1 = simply annulated, 2 = divided.
47. Type of cuticular subdivision or annulation, excluding head: 0 = not applicable, 1 = homonomy (all segments or subdivisions about equal in size), 2 = heteronomy.
48. Trilobation: 0 = not applicable, 1 = absent, 2 = present.
49. Thoracic pleurae: 0 = absent, 1 = present.
50. Pleural fusion: 0 = not applicable, 1 = pleurae unfused, 2 = posterior pleurae fused into pygidium, 3 = all pleurae fused into thoracic shield.
51. Pleural direction: 0 = not applicable, 1 = all pleurae more or less orthogonal to body, 2 = increasing curvature of pleurae posteriorward.
52. Pleural overlap: 0 = not applicable, 1 = no overlap, 2 = overlap.
53. Division of cuticle along central midline: 0 = absent, 1 = present.

54. Trunk papillae: 0 = absent, 1 = present, 2 = enlarged into appendicules.
55. Enlarged dorsal bosses: 0 = absent, 1 = simple bosses, 2 = enlarged plates.
56. Dorsal bosses paired: 0 = not applicable, 1 = unpaired, 2 = paired, 3 = triple.
57. Paired dorsal plate position: 0 = not applicable, 1 = lateral, not touching dorsally, 2 = dorsal, touching or nearly touching.
58. Dorsal boss spines: 0 = not applicable, 1 = non-spinous, 2 = spine extending from center, 3 = fine spine extending from posterior margin, 4 = "fin rays" (autapomorphic for *Nectocaris*).
59. Other boss ornament: 0 = not applicable, 1 = smooth, 2 = reticulate, 3 = sulcate (autapomorphic for *Cardiodictyon*).
60. Number of bosses (if single) or pairs (if paired) per body segment: 0, 1, 2, 3.
61. Terminal boss or boss pair: 0 = not applicable, 1 = present, 2 = lost.
62. Tracheae: 0 = absent, 1 = present.
- Hou and Bergström (1995) speculated that the numerous long papillae of the Cambrian lobopod *Onychodictyon* would have had a respiratory function and that these papillae could have been transformed into tracheae by being turned inside out. I chose not to homologize tracheae with papillae. However, the idea could be tested using more information on the development of extant insect and myriapod tracheae and of extant onychophoran tracheae and dermal papillae.
63. Paired midgut diverticulae: 0 = absent, 1 = present.
64. Central body separated from appendages by joint or cuticular fold: 0 = not separated, 1 = separated.
65. Posterior appendages: 0 = not applicable, 1 = all abdominal appendages present, 2 = reduction of last pair to spine (autapomorphic for *Burgessia*), 3 = reduction of several to vestigial (autapomorphic for *Dasyleptus*), 4 = complete loss of several pairs.
66. Differentiation of posterior portion of body: 0 = none, 1 = abdominalization, 2 = extreme reduction or loss.
67. Position of anus: 0 = terminal, between last appendages, 1 = terminal, on an extension of the body past the last pair of appendages, 2 = ventral, on terminal body division, 3 = ventral, on penultimate body division.

In most Vendian fossils, the anus cannot be seen at all. However, the only specimen of *Mialsemia* is fortuitously broken and shows what is probably the hindgut, extending to the posterior tip of the body.

68. Uropods: 0 = not applicable, 1 = absent, 2 = present.
69. Telson: 0 = absent, 1 = present.
70. Telson type: 0 = not applicable, 1 = buttonlike, 2 = flattened, 3 = styliform.
71. Paired ventral plates in addition to/instead of single sternite: 0 = absent, 1 = present.

Ventral plates are not always easy to assess in fossil material. Chen et al. (1994) called attention to paired ventral plates of some sort in anomalopods. They made a strong case that the posited "lobo-

pods" of *Kerygmachela* (Budd, 1993) could not have been appendages but were ventral plates of some sort. (I have followed this interpretation for now but have not seen the fossils and may need to revise my opinion.) It might be possible to homologize these ventral plates with the ventral bosses of palaeoscolecid, as Dzik (1991) homologized the dorsal bosses of armored lobopods with palaeoscolecid dorsal bosses. Taken to its conclusion, this approach would homologize palaeoscolecid bosses with lobopod dorsal plates, arthropod limbs, and paired ventral plates of various taxa but for now is too conjectural.

72. Paired caudal cirri: 0 = absent, 1 = unsegmented, 2 = segmented.

I hypothesize homology among the cirri of kinorhynchs, the caudal alae of some heterotardigrades, and the furcae of some arthropods and anomalopods. Delle Cave and Simonetta (1991) called all structures derived from dorsal postanal embryonic material a telson; by this definition, caudal cirri or furcae would be either "legs" or a "telson." They noted that the embryological origin of arthropod furcae are not well known. However, well-developed caudal cirri or furcae are present in organisms such as kinorhynchs, to which this definition is hard to apply. I thus prefer not to homologize cirri with either appendages or a telson.

73. Caudal cirri morphology: 0 = not applicable, 1 = straight and unbranched, 2 = forked or branching.
74. Cuticular sclerotization: 0 = unsclerotized, 1 = only appendages sclerotized, 2 = most of cuticle sclerotized.

I have gauged the degree of cuticular sclerotization by the inferred flexibility, resistance to deformation, and where applicable the relief of the fossil. Cuticular structure and composition is likely to be homologous among living arthropods (Cutler, 1980), and the cuticles of living tardigrades and kinorhynchs show definite similarities with those of arthropods (Kristensen and Higgins, 1991; Kinchin, 1994), but lack of definite information for fossil taxa precluded the scoring of more than this very general character.

75. Mineralization of cuticle: 0 = unmineralized, 1 = mineralized with CaCO_3 , 2 = mineralized with CaPO_4 .

Note added in proof.—Several recent studies bear on the results presented here. Collins (1996) has presented new data on *Anomalocaris*: the organism called *Peytoia* in this paper is now considered a junior synonym of *Laggania*. Collins agreed that the anomalocarids and their kin are arthropods; he proposed the name Dinocarida for the taxon that I named Anomalopoda. Collins also stated that the proposed connection between *Anomalocaris* and *Kerygmachela* is extremely tenuous. Two new molecular analyses (Winnepenninckx et al., 1995; Garey et al., 1996) support "aschelminth" paraphyly, with priapulids as an outgroup to the arthropods and their allies, and confirm the separation of the annelids and arthropods. Garey et al.'s results also sup-

port the position of the tardigrades as an outgroup to the euarthropods.

COLLINS, D. 1996. The "evolution" of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.) J. Paleontol. 70: 280–293.

GAREY, J. R., M. KROTEC, D. R. NELSON, AND J. BROOKS.

1996. Molecular analysis supports a tardigrade–arthropod association. Invert. Zool. 115:79–88.

WINNENPENNINCKX, B., T. BACKELJAU, L. Y. MACKAY, J. M. BROOKS, R. DE WACHTER, S. KUMAR, AND J. R. GAREY. 1995. 18S rRNA data indicate that Aschelminthes are polyphyletic in origin and consist of at least three distinct clades. Mol. Biol. Evol. 12:1132–1137.

APPENDIX 3

Data set used in this analysis, with inapplicable characters scored as a separate "not applicable" character state.

<i>Praecambridium</i>	131101110101102000000112111211100??11??0?222?0010000000000000?010?11100020
<i>Parvancorina</i>	13110??01011010000001120112121?01?11??0?22??0010000000000000?1?0?10000020
<i>Vendia</i>	13110111010110000000112011211100??11??00222?00000001012111120?010?10000020
<i>Mialsema</i>	131102?02101100??0?1220112111?0??00222?00000000000000010010000020
<i>Bomakellia</i>	131102?02??1100111111220000011?0??00223?210000000121112?0?110?0??0?020
<i>Spriggina</i>	111101110101100000001221000011000?11??00225?2100000000000000?110?10000000
<i>Marywadea</i>	1111011010110200000122000011000?11??00225?2100000000000000?110?10000000
<i>Peytoia</i>	13110230223210011211112200000114013211100323021000000000000000110020011110
<i>Anomalocaris</i>	13110230210310011211112200000114013211100323021000000000000000110010011110
<i>Opabinia</i>	1322121312311001222111210000011101421?00?124?21000000000000000110021211100
"C-monster"	13110113021301000000000000000000000110000123011000001011021220?110010000000
<i>Nectocaris</i>	131100110101100112112121012111120?111??0?005?110000010110413?0?40?0000??00
<i>Facivermis</i>	131100130101100000000000000000000500111??00025011000000000000000110100000000
<i>Onychodictyon</i>	1311011302123100000000000000000111110000113112000000122221200010010000000
<i>Aysheaia</i>	1311011302225100000000000000000100321000011311100000100000000010010000000
<i>Luolishania</i>	131101130101410000000000000000010111?000323?120000001131111000010110000000
<i>Hallucigenia</i>	131101110221310000000000111111301101001011200000000022121120?010110000000
<i>Microdictyon</i>	131101110??12100000000000000000010110100101130000000000221121200010110000002
<i>Cardiodictyon</i>	131101110??141000000000000111111301101?010?15100000000222131100010110000000
<i>Xenusium</i>	131101130102??00000000000000000001010010324111000001122121110?010010000000
<i>Kerygmachela</i>	131102132102100000000111000001010?421??0012301200000010000000?110010012100
<i>Marrella</i>	13221330010121100001012101111222211110001225021000000000000000110111100020
<i>Sidneyia</i>	132413300103100112112122011112111121100011230210112200000000000141221200020
<i>Canadaspis</i>	1322133001011001121111210122111521211000111502100000000000000014111101120
<i>Skara</i>	1322133001011000000012101111215212110001014021100000000000000?140101102220
<i>Olenoides</i>	13221330010321211112112211122241121100011240211122200000000001111211102121
<i>Agnostus</i>	132213300103212000001122111112241121100011120211122100000000001111211100021
<i>Naraoia</i>	132213300101102000001221111121411211000?224021113220000000000110211100021
<i>Cheloniellon</i>	13221330010110011102112201111215212110001124021111220000000000110?11201120
<i>Sanctacaris</i>	1322233001021001111121221111121611311000?124021011112011211112001?1321200020
<i>Burgessia</i>	132313300101102000001221112111411511000123021000000000000001120311300020
<i>Yohoa</i>	1324233001011001121121230111112400312000121402101112000000000000141211200020
<i>Leancoilia</i>	132213300102223000000121011111313011120000213021211220000000000111311300020
<i>Palaeoisopus</i>	131103300102210123211121000001042031100102230210000000000000001141311300020
<i>Dasyleptus</i>	131103300101100111111121000001031131100012140210000000000000001013021130?020
<i>Arthropleura</i>	1311033001031000000012100000102113110000125?2111122010000000?110211210020
<i>Echinoderes</i>	00000000000000000000012100000000000011000030210000011111311100100000012120
<i>Semnoderes</i>	0000000000000000000001210121110000001100003021000001113131100100000012120
<i>Priapulid</i>	000000000000000000000110000000000001100000011000000100000000000000000000
<i>Macrobotus</i>	121101110211320000000111000000000010011001110100000000000000000210000000
<i>Milnesium</i>	12110111021132000000011000000000010011002111110000000000000000110010000000
<i>Echiniscus</i>	13110112021241000000012200000000010001001111210000002223212011100100?1120
<i>Echiniscoides</i>	1311011202125100000001210000000001000100121121000000000000001110010001120
<i>Neostygarctus</i>	131101120213410000000121000000000100010012112101111011132212011100100002120
<i>Peripatus</i>	13110113010131000000011100000000311311000112411100000010000001001011000000
<i>Lithobius</i>	13110330010110000000121000001041131100011250220000000000000101011102120
<i>Nymphon</i>	13110330010121012311111100000004103110010122021000000000000001142110000020

APPENDIX 4

Recoding of data set used in this analysis, with inapplicable characters scored as missing (?).

<i>Praecambridium</i>	1311?111?1?11?20?????112111211100??11??0?222??10???000?????0?0?010?11100?20
<i>Parvancorina</i>	1311?????1?11?10?????1120112121?01?11??0?222????10???0000?????0?0?1?0?10?00?20
<i>Vendia</i>	1311?111?1?11?00?????112011211100??11??00222??10???0101211120?010?10?00?20
<i>Mialsemia</i>	1311?2??21?11?0?????1220112111?0?????00222??10???0000?????0?0?00110010?00?20
<i>Bomakellia</i>	1311?2??2?1?1?01111112200??11?0?????00223?21?0???00121112?0?110???0?0?20
<i>Spriggina</i>	1111?111?1?11?00?????12210???11000?11??00225?21?0???0000?????0?0?110?10?00?00
<i>Marywadea</i>	1111?111?1?11?20?????12200??11000?11??00225?21?0???0000?????0?0?110?10?00?00
<i>Peytoia</i>	1311?23?22321?011211112200??114013211100323021?0???0000?????0?0?00110020?11110
<i>Anomalocaris</i>	1311?23?21?31?011211112200??114013211100323021?0???0000?????0?0?00110010?11110
<i>Opabinia</i>	1322121312311?012221112100??11101421?00?124?21?0???0000?????0?0?110?10?00?00
"C-monster"	1311?113?1?31?00?????0?0?00?????0001110000123011?0???1011?21220?110010?00?00
<i>Nectocaris</i>	1311??11?1?1?0112112121012111120?111??0??5?11?0???1011?413?0??40?0?0?00
<i>Facivermis</i>	1311??13?1?1?1?00?????0?0?00?????500111?0?0?25011?0???0000?????0?0?001101?0?00?00
<i>Onychodictyon</i>	1311?113?2123100?????0?0?00?????1111110000113112?0???01222221200010010?00?00
<i>Aysheaia</i>	1311?113?2225100?????0?0?00?????1003210000113111?0???010?????0?0?00010010?00?00
<i>Luolishania</i>	1311?113?1?14100?????0?0?00?????010111?000323?12?0???01131111100010110?00?00
<i>Hallucigenia</i>	1311?111?2213100?????0?0?01111113011?100101120???0???0022121120?0101010?00?00
<i>Microdictyon</i>	1311?111???12100?????0?0?00?????1011?100101130???0???00221121200010110?00?02
<i>Cardiodictyon</i>	1311?111???14100?????0?0?01111113011?1?010?151???0???00222131100010110?00?00
<i>Xenusion</i>	1311?113?1?2?00?????0?0?00?????0001?10010324111?0???1122121110?010010?00?00
<i>Kerygmachela</i>	1311?21321?21?00?????11100??1?1?0?421??00123012?0???010?????0?0?110010?12100
<i>Marrella</i>	1322133??1?12110??1?121011122221110001225021?0???0000?????0?0?00110111100?20
<i>Sidneyia</i>	1324133??1?31?01121121220111211112110001123021?1122000?????0?0?00141221200?20
<i>Canadaspis</i>	1322133??1?11?011211112101221115212110001115021?0???0000?????0?0?0014111101120
<i>Skara</i>	1322?33??1?11?00?????12101111215212110001?1402110???0000?????0?0?1401?1102220
<i>Olenoides</i>	1322133??1?32121111211221111222411211000112402111222000?????0?0?01111211102121
<i>Agnostus</i>	1322133??1?32120?????11221111122411211000111202111221000?????0?0?01111211100?21
<i>Naraoia</i>	1322133??1?11?20?????1221111121411211000?22402111322000?????0?0?01110211100?21
<i>Cheloniellon</i>	1322133??1?11?0111?211220111121521211000112402111122000?????0?0?00110?11201120
<i>Sanctacaria</i>	1322233??1?21?01111121221111121611311000?124021?1112011211112001?1321200?20
<i>Burgessia</i>	1323133??1?11?20?????12211121114115110000123021?0???0000?????0?0?01120311300?20
<i>Yohoia</i>	1324233??1?11?011211212301111124003120001214021?1112000?????0?0?00141211200?20
<i>Leancoilia</i>	1322133??1?22230?????1210111131301112000021302121122000?????0?0?00111311300?20
<i>Palaeoisopus</i>	1311?33??1?221012321112100??1?4203110010223021?0???0000?????0?0?01141311300?20
<i>Dasyleptus</i>	1311?33??1?11?011111112100??1?3113110001214021?0???0000?????0?0?1013021130??20
<i>Arthropleura</i>	1311?33??1?31?00?????12100??1?2113110000125?2111122010?????0?0?110211210?20
<i>Echinoderes</i>	0?????????????00?????12100?????000??1100??3021?0???11113111001?00?0?12120
<i>Semnoderes</i>	0?????????????00?????1210121111000??1100??3021?0???111313111001?00?0?12120
<i>Priapulid</i>	0?????????????00?????11100?????000??1100?00011?0??010?????0?0?000?00?0?00?00
<i>Macrobiotus</i>	1211?111?2113200?????11100?????0001??11001111?1?0???0000?????0?0?000?0210?00?00
<i>Milnesium</i>	1211?111?2113200?????11100?????0001??1100211111?0???0000?????0?0?00110010?00?00
<i>Echiniscus</i>	1311?112?2124100?????12200?????0001??0100111121?0???00222321201110010??1120
<i>Echiniscoides</i>	1311?112?2125100?????12100?????0001??0100121121?0???0000?????0?0?01110010?01120
<i>Neostygarctus</i>	1311?112?2134100?????12100?????0001??0100121121?111101113221201110010?02120
<i>Peripatus</i>	1311?113?1?13100?????11100?????3113110001124111?0???010?????0?0?10010110?00?00
<i>Lithobius</i>	1311?33??1?11?00?????12100?????14113110001125022?0???0000?????0?0?10110111102120
<i>Nymphon</i>	1311?33??1?121012311111100?????4103110010122021?0???0000?????0?0?01142110?00?20